



IMPERIAL INSTITUTE
OF
AGRICULTURAL RESEARCH, PUSA.

THE OHIO JOURNAL OF SCIENCE

Official Organ of the

OHIO ACADEMY OF SCIENCE

and of the

OHIO STATE UNIVERSITY SCIENTIFIC SOCIETY

VOLUME XXIV — 1924

OHIO STATE UNIVERSITY

COLUMBUS

THE OHIO JOURNAL OF SCIENCE

VOL. XXIV

JANUARY, 1924

No. 1

A TAXONOMIC, ECOLOGIC AND ECONOMIC STUDY OF OHIO APHIDIDÆ.*

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INTRODUCTION.

The Aphididæ constitute a very interesting group of insects. From a biological point of view their peculiar mode of reproduction, together with their complicated life cycle give them special interest among insects. The taxonomy of the family is very much complicated because of the great variation of forms which occur even within the same species. The annual loss occasioned by the feeding habits of the family places the group in a major position economically.

The author began the study of the family in the summer of 1915 while a student at Ohio State University, Lake Laboratory, Cedar Point, Ohio. Since that time much time has been spent in collecting, mounting and identifying species, together with field work in study and control of several destructive species. Special study was made of the life cycle of *Macrosiphum solanifolii* for one season while the author was employed as an assistant at Ohio Agricultural Experiment Station. In this study attention was given to the seasonal change of host plants of this species and factors which seemed to affect migration.

Collections were followed with color notes of the species. In addition to the Ohio forms studied, over two hundred species

* Dissertation presented in partial fulfillment of the requirements for the Degree of Doctor of Philosophy in the Graduate School of the Ohio State University.

collected in Pennsylvania have been studied and color notes and habit descriptions made. These notes are much too lengthy to include in this work, but it is expected that they may be incorporated in future papers dealing with the group. The following outline has proven of much help in making and keeping records of collections:

Name.....	Number.....
Place of Collection.....	Date.....
Collector.....	Ants attending.....
Host plant.....	Notes.....
Literature.....	

On the reverse side of the sheet is an outline for color notes:

General color.....	Head.....
Thorax.....	Abdomen.....
Antennae.....	Legs.....
Wings.....	Cornicles.....
Cauda.....	Notes.....

The author finds a five by eight loose-leaf note book opening lengthwise satisfactory for this outline.

Each collection is given a number which is recorded on the note sheet and on each slide mount made. This same number may be used for insects taken in association with the Aphid species.

For the most part the species collected have been mounted directly into balsam without special clearing. In place of xylol, which is usually used as a solvent for the balsam, the author prefers toluene, since it seems to serve as a better clearing agent than the xylol and the mounts dry more quickly. The balsam is made quite thin by the addition of toluene and a drop placed on a clean microscope slide. The living aphid is then placed in this drop, and after wetting with a small drop of toluene is spread to show body parts. The cover glass is put in place and the space well filled with balsam.

The slides are then placed in a drying oven kept at a temperature of from 40 to 45 degrees C. Certain dark-colored species must be cleared before permanent mounts are made. In fact, many workers in the group are now clearing all their specimens in potassium hydroxide before mounting.

The literature for the Family has been reviewed and the source of latest information as to synonymy and the like for each species is inserted after the name of the species in the list given for the state.

ACKNOWLEDGMENTS.

The author is indebted to many persons for help in this work. Mr. P. R. Lowry, New Hampshire Agricultural College, collected many specimens and made several color descriptions. Professor H. A. Gossard, Ohio Agricultural Experiment Station, gave many helpful suggestions, and gave liberally of time in helping in this study. Doctor A. C. Baker, United States Department of Agriculture, identified many species, and checked over identifications made by the author, giving most freely of his time and knowledge. Doctor R. C. Osburn, Head of the Department of Zoology and Entomology, Ohio State University, gave much encouragement and aid. Professor J. G. Sanders, Director of Pennsylvania Bureau of Plant Industry, has offered every facility for the pursuit of this study and has always stood ready to aid. He has given valuable aid in reading and criticizing this manuscript. To all these the author gives his hearty thanks. To Doctor Herbert Osborn, Ohio State University, under whom this work has been done, special thanks are due for aid and encouragement, and for his enduring belief in the author's ability to pursue the work. To him would I dedicate this work.

TAXONOMY.

The family Aphididæ belongs to the Order Hemiptera, Suborder Homoptera of the Class Insecta. The Homoptera are divided into two groups according to the manner in which the rostrum is placed in relation to the sternum of the prothorax. First, the families with the rostrum free from the sternum known as the Auchenorhynchi. This group embraces the families Cicadidæ, Fulgoridæ, Membracidæ, Cercopidæ, and Cicadellidæ. The second group is made up of the families in which the beak is fused with the sternum of the prothorax, known as the Sternorhynchi, embracing the families Psyllidæ, Aphididæ, Aleurodidæ, and Coccidæ.

Relationships of the families of the Sternorhynchi will be discussed under the following topics: General body shape, structure and position of the rostrum, antennal comparison, leg structure, presence of wax glands, wing venation, and reproduction.

General Body Shape.

In general body shape the Psyllidæ closely approach the Cicadidæ, and it would seem as though some Cicada-like stock gave rise to the Psyllid group. Certain mature forms of the family Aleurodidæ have a resemblance to Psyllidæ. This type form has been greatly modified in the nymphal forms of the family where sedentary habit and coccid-like forms are associated. Aphididæ show less divergence from the Psyllid type than do the Aleurodidæ, and excepting the dimorphs of certain forms (*Periphyllus* sp. and others) and scale-like individuals belonging to the genera Chermes, Cerataphis, and Phylloxera, the developing nymphs resemble the adults in body form. The Coccidæ have digressed farthest from the primitive ancestral stock of the Sternorhynchi; this is particularly marked in the females of the Diaspinæ. Loss of body parts and change in general shape is marked throughout the family, undoubtedly associated with the more or less sedentary habits of the species.

Morphology and Position of the Rostrum.

The rostrum of the Psyllidæ is long, though never as long as the body, and is composed of three segments. It is of the ordinary Hemipterous type. In the Aphididæ the segments of the rostrum number four or five, and this segmentation is characteristic of the family, this number not occurring in other families of the Hemiptera. The rostrum has shortened in the Aleurodidæ and is composed of three segments, while with the Coccidæ there is a sex difference in the structure of the rostrum. In the male it is usually spoken of as being absent, but it is represented by a minute triangular projection, the labium; while in the female the rostrum is well developed. Here the mandibles and maxillæ are bristle-like and often much longer than the body. Mouth-parts are lacking in adult females of the two subfamilies Margarodinæ and Xylococcinæ.

Antennal Condition.

Well developed, filiform antennæ are always present in the Psyllidæ. The segments tend to be uniform in size and are from nine to twelve in number, and are without sensoria. The attachment to the head is in front of and somewhat below the eyes. Antennæ are always present in the Aphididæ, attached to the front of the head. They are usually somewhat

conspicuous and consist of from three to six segments, with the last segment frequently fitted with a filamentous prolongation or spur. Sensoria and sensilia are characteristic of the aphid antennal segments. The sensoria are probably organs of special sense, and their position, number and shape are of generic and specific significance. Antennæ are always present in the Aleurodidæ, attached to the front of the head. Sensoria are lacking. The presence or absence, and number of segments in the antennæ of the members of the family Coccidæ depends upon the genus and sex of the individual. With the male the organs usually are present and made up of about ten segments, with attachment to the front of the head. With the female the antennæ may be composed of as many segments as the male or the number may be greatly reduced. Attachment is to the under side of the body. Sensoria are lacking in both sexes.

Leg Structure.

Associated with the jumping habit of the Psyllidæ are the swollen hind femora. The tarsi are two-jointed. The legs of Aphididæ are long and slender, except in dimorphic forms and the Phylloxerina where the legs are greatly shortened, suggesting the condition found in the Coccidæ. Typically there are two tarsal segments in the Aphididæ though in the genus *Mastopoda* both segments and claws are lacking.

Legs are always present in the adult Aleurodidæ, but are lacking in the nymphal forms. In the late nymphal stage the developing legs of the adult may be seen on the ventral side of the body, but are within the insect's pupal case and non-functional. Male Coccidæ have well developed legs, fitted with single jointed tarsi which terminate in a single claw. The males of two species of the genus *Exaeretopus* are exceptions to the above, and bear tarsi of two segments. The female of some genera of Coccidæ bear legs while in other genera they do not. Ordinarily their legs do not project beyond the sides of the body. Tarsi are, as in the male, single jointed and single clawed.

Wax Glands.

Wax secreting glands are found in all the families of the Sternorhynchi. In Psyllidæ oval wax glands are found in the adult *Trioza salicis*. Abdominal and marginal glands are

found in nearly all nymphal stages. These marginal pores secrete long fine hollow waxen hairs which sometimes form a conspicuous fringe about the insect. Some nymphal forms of Aleurodidæ have wax pores of different types, such as simple, agglomerated, and compound. Dorsal pores are present and are always simple, and may be arranged in definite rows producing a ring comparable to that in the nymphal form of Psyllidæ. In the Aphididæ the wax glands are grouped. Eriosoma and some Pemphigus show a simple ring grouping, while in the Chermes and Mindarus the pores have agglomerated, and in some instances are surrounded by a chitinized ring. Secretion of wax is most marked in the mature forms. Wax secretion and wax pores probably reach the greatest development in the Coccidæ, forming the greater part of the armor of soft scales. The freshly hatched nymph shows no signs of waxy secretions, but eventually waxen threads start growing over the whole of the body surface. The development of wax probably is most pronounced in the genera Ceroplastes and certain Tachardias. The production of wax increases with the increase of sedentary habit in the families of the group. The protection offered by the wax has undoubtedly added much to the success of the families in the protection afforded from enemies and adverse weather conditions.

Wing Venation.

The entire discussion of wing tracheation and venation is based on the work of Doctor Edith M. Patch "Homologies of the Wing Veins of the Aphididæ, Psyllidæ, Aleurodidæ and Coccidæ," Vol. II, p. 101-129, An. Ent. Soc. of Amer.

There is a specialization in the group through the loss of parts of wings even to their total loss. Adults of the family Psyllidæ always bear two pairs of wings. Nymphal tracheation shows seven tracheae in the fore wing as follows: Costal, subcostal, radial, medial, cubital, first anal and second anal. Newly emerged wings show the following condition: Costal tracheation has disappeared, subcostal tracheae have migrated to near the costal margin, the proximal one-fourth of the radial, medial, and cubital tracheae have coalesced, the first anal follows the course of the claval suture, while the second anal has migrated to near the anal margin.

Mature forms of the family Aphididæ may be either winged or wingless in the same species; or entirely without wings, so far as is known, throughout the life cycle. The wings for the most part are clear, and always consist of two pairs, with the front pair considerably larger than the hind pair. Aphididæ in the more generalized genera have four nymphal tracheae: Radial, medial, cubital and first anal. In the newly developed wing the tracheae are reduced to two, one carrying the radial and radial sector; the other the medius, cubitus and anal. The costa and subcosta are probably not preceded by tracheae. In the *Chermes*, a genus probably showing specialization, there seems to be an unstable condition of tracheation from two basal tracheae to a single basal trachea. In newly emerged *Chermes* wings the radius has disappeared and the radial sector has straightened out to occupy the caudal margin of the stigma; the medius has migrated to the position usually occupied by the radial sector.

The wings of the Aleurodidæ are always four in number. The venation is greatly reduced. There are four pairs of the fine but distinct tracheae, the costal, subcostal, radial and cubital; all extending separately to the base of the wing. The medial trachea is indicated by a very faint tracing in the wing. In the definitive venation of the fore wing the costa, subcosta, veins radius one and the media are lacking; only the main stem of the radius and radial sector, and cubitus are developed. The hind wing has but one vein which is probably the radius and radial sector.

Wings are lost in the Coccidæ except in the male, where they are represented by a single pair (the fore pair, the hind wings being represented by a pair of hooks). Tracheation of the wings in the male of *Dactylopius* is represented by four distinct tracheae. These tracheae remain distinct until after the veins have begun to form so that the relation of the two is at once seen. There seems no necessary connection between the tracheae and the veins which are found later.

Reproduction.

Reproduction becomes more specialized from the Psyllidæ to the Coccidæ. Psyllidæ reproduce oviparously and as a rule are single brooded in a year. Aleurodidæ reproduce oviparously with two or more broods each year. In the Aphididæ reproduc-

tion may be oviparously, or viviparously and parthenogenetically, or oviparously and parthenogenetically. In a great number of genera several viviparous parthenogenic generations follow one after the other throughout the favorable growing season, and upon the arrival of a season of unfavorable growth produce "true sex" forms, the females of which after copulation lay the overwintering eggs. From these eggs hatch young which are all females—the beginning of the viviparous parthenogenetic generation—the "stem mothers." Coccidæ reproduce oviparously, viviparously and a few probably parthenogenetically; and with several generations each year.

Viviparous and parthenogenetic conditions have arisen independently in the different families as we have in each family primitive oviparous forms showing that this habit was retained until after the separation of the different family offshoots from the common stock.

Summary of Relation of Families of Sternorhynchi.

From the foregoing topical comparisons it is evident that the Psyllidæ are nearest to the primitive ancestral form from which the Sternorhynchal stem branched. The resemblance in body form and organ structure of the Psyllidæ to the less specialized Auchenorhynchi is quite marked. As shown under the discussion of wing venation and wing structure there is a specialization from the well developed wing condition of Psyllidæ to a wingless condition, as found in certain Aphididæ and Coccidæ.

The families Aleurodidæ, Aphididæ and Coccidæ are further removed from the ancestral stock showing specialization through loss of body parts associated with the sedentary life habits, and the departure from the primitive or true Hexapod mode of reproduction.

From the stem of the primitive ancestral form the Psyllidæ were the first to branch off and the other families diverged higher up on the stem, the three at about the same time, each specializing in its own way; the Aphididæ in the matter of reproduction, development of antennal sensoria, abdominal cornicles and beak segmentation; the Aleurodidæ in greatly specialized nymphal forms; the Coccidæ in loss of body parts and in specialized reproduction.

CHARACTERISTICS OF THE APHIDIDÆ.

At present there are about eight or ten hundred described species of Aphididæ. The members of the family may be characterized as follows: Body soft, more or less oval, appendage tending to be long and slender, wings when present membranous and two pairs in number, mouth parts sucking in type, antennal segments from three to six, segments bearing sensoria and sensilia, tarsi two-jointed, abdomen bearing on the fifth segment a pair of dorsi-lateral cornicles, reproduction both by parthenogenesis and amphigony.

CLASSIFICATION OF THE APHIDIDÆ.

In this work the Family Aphididæ is divided into five subfamilies as follows: Aphidinæ, Mindarinæ, Hormaphidinæ, Eriosomatinae and Phylloxerinae. Dr. A. C. Baker in his work on generic classification* set up a superfamily Aphidoidea and separated this into two families, Phylloxeridae and Aphididae. This classification to the writer seems unnecessary and adds to confusion in the group. It seems evident to the writer that the Phylloxerinae comprise the more specialized group of the family. The parthenogenetic oviparous mode of reproduction of the Phylloxerinae probably developed from the parthenogenetic viviparous mode of the other subfamilies, and may be considered an advance over the other subfamilies. The loss of body parts has gone farther in the Phylloxerinae, as shown in the loss of antennal segments, probable loss of cornicles, modification and loss of wing venation, than in the other subfamilies. There is a similarity in the galls formed by the Phylloxerina and those of Hormaphidinæ and wax plates and glands are evident in the subfamily. The sex forms of the genus Phylloxera are quite suggestive of Eriosomatinae in being beakless, apterous, dwarfed in size and the female laying a single fertilized egg.

The key to the subfamilies, using Baker's work as a basis, would be as follows:

Key to the Subfamilies of the Aphididae.

1. "Summer parthenogenetic oviparous forms produced. Stigma formed by the radial sector.....Phylloxerinae
Only sexual oviparous forms produced, stigma formed by radius.....2

* Bull 826, U. S. D. A. 1920, p. 2.

2. "Sexual forms small with functioning mouth parts absent. Oviparous females with all the egg tubes present or indicated in the embryo but the adult possessing only one tube and maturing one cell so that one egg only is laid. Cornicles much reduced or absent. Wax glands abundantly developed. Wind veins usually reduced. Antennal sensoria prominent.
Eriosomatinae
- "Sexual forms with functioning mouth parts. Nearly all the ovarian tubes developed in the adult oviparous female.....3
3. Radial sector of forewing inserted mesad of the stigma. Sexes small. Oviparous female laying several eggs.....Mandarinae
Radial sector not so inserted, but arising from the stigma.....4
4. "Forms usually gall makers. Wing veins much reduced so that the media is usually simple. Wax glands usual. Antennal sensoria annular, Aleurodiform stages common. Sexes wingless as a rule and small..Hormaphidinae
"Forms not usually gall makers. Wing veins often not reduced. Wax glands not abundant. Antennal sensoria oval or subcircular. Aleuridiform stages rare. Cornicles often little reduced. Winged males common.
Aphidinae

Baker's keys to the genera of the four subfamilies Eriosomatinae, Mandarinae, Hormaphidinae and Aphidinae have been followed in classification.

The Subfamily Phylloxerinae is characterized as follows:

Biological characters: Gall forming on conifers and the leaves of deciduous trees and woody plants. Reproduction so far as known entirely by eggs.

Morphological characters: Radial sector of wing forming the caudal margin of the stigma; the radius has disappeared and the media has taken the place occupied by the radial sector in the more generalized groups. Fundatrix with three antennal segments. Cornicles wanting.

The subfamily may be separated into two tribes by the following key:

1. Cubitus arising from the first anal vein about one-third distance from its proximal end. Gonapophysis absent.
Gall forming on the leaves of deciduous trees and woody plants.....
Tribe Phylloxerini
- Cubitus arising from stigma independent of the anal vein.
Gonapophysis represented by three short cone-like bodies. Found on conifers.
Tribe Chermisini

Tribe *Phylloxerini*

Biological characters: Most species gall forming on leaves and roots of deciduous trees and woody plants. Reproduction by eggs. Sexual forms known.

Morphological characters: Head rounded in front; thoracic region broad; abdomen somewhat conical in the alate. Antennae short with three segments, the third being much the longer. Beak moderately long; absent in the sexuals. Wings rather large, cubital arising from the first anal. Tarsal sensilla long and capitate. Cornicles wanting. The tribe embraces the genus *Phylloxera* Boyer with *P. quercus* Boyer as type.

Tribe *Chermisini*.

Biological characters: Found on coniferous trees and at times causing galls on the host plant. Reproduction by parthenogenetic oviparous eggs only. Male form not definitely known.

Morphological characters: Apteræ with broad oval body. Antennae very short and three jointed. Legs short and stout. Beak stout and with very long setae. Entire body with a large number of glandular patches. Antennae of alate apparently of five segments. Head very broad. Suckers at distal end of tibiae. Cubitus arising from stigma independent of the anal vein. Gonapophysis represented by three short cone-like bodies.

The tribe embraces the genus *Chermes* Linn. with *C. abietis* Linn. as type.

LIST OF OHIO SPECIES.

The known Ohio representatives of the family Aphididæ are given in the following list together with bibliographical references as to synonymy, description and life habits.

Subfamily APHIDINÆ.

Tribe Lachnini.

ANOECINA.

Anoecia querci (Fitch). Ent. News, Vol. 27, p. 359. In migration. Winterset, Oct. 20, 1916.*

SCHIZOLACHNINA.

Dilachnus strobil (Fitch). Described as *Lachnus strobil*, now considered as coming in the genus *Dilachnus* as defined by Baker. Can. Ent., Vol. 51, pp. 211 and 253. Columbus, Ohio. Reported by H. Osborn.

Schizolachnus rosea (Choldk.). Described as *Lachnus rosea*. European form. On wild rose. Wooster, Ohio. Oct. 29, 1917. Oviparous females taken.

LACHNINA.

Lachnus sp. Identified as a new species by Mr. H. F. Wilson. Specimen retained to be described by himself. Columbus, Ohio. May 21, 1915. W. W. Marshall, Coll.

Longistigma caryæ (Harris). Can. Ent., Vol. 41, p. 385. Common throughout the state in the fall on sycamore (*Platanus occidentalis*).

Tribe Callipterini.

PHYLLAPHIDINA.

Phyllaphis quercicola Baker. Ent. News, Vol. 27, p. 362, and Vol. 22, p. 241. White oak (*Quercus alba*). Wooster. July 4, 1920. P. R. Lowry, Coll.

Phyllaphis fagi (Linn.) Bul. 826, U. S. D. A., 1920, p. 24. On beech (*Fagus americana*). Wooster. August 19, 1920. P. R. Lowry, Coll.

CALLIPTERINA.

Therioaphis tiliæ (Linn.) Bul. 826, U. S. D. A., 1920, p. 28. On linden (*Tilia americana*). Columbus. October 12, 1916.

Euceraphis mucidus (Fitch). Jr. Ec. Ent., Vol. 10, 1917, p. 425. Sugar Grove. September 3, 1912. W. W. Marshall, Coll.

Monellia caryæ (Monell). Jr. Ec. Ent., Vol. 10, 1917, p. 424. On black walnut (*Juglans nigra*). Winterset. August 11, 1916.

Monellia caryella (Fitch). Jr. Ec. Ent., Vol. 10, 1917, p. 424. On shingle oak (*Quercus imbricaria*). Winterset. August 11, 1916.

* Species listed without collector name were collected by the author.

Calaphis betuella Walsh. Proc. Wash. Ent. Soc., Vol. 18, 1916, p. 185. On *Betula papyrifera*. Wooster. August 7, 1917.

Calaphis betulaecolens (Fitch). Proc. Wash. Ent. Soc., Vol. 18, 1916, p. 186. On *Betula lutea*. Wooster. September 11, 1917.

Calaphis castaneæ (Fitch). Proc. Wash. Ent. Soc., Vol. 18, 1916, p. 187. On *Aesculus hippocastanum*. Wooster. September 20, 1917.

Calaphis annulata (Koch.). Jr. Ec. Ent., Vol. 10, p. 427. On *Betula alba*. Wooster. August 7, 1917.

Myzocallis asclepiadia (Monell). Jr. Ec. Ent., Vol. 10, p. 423. On milkweed (*Asclepias syrica*). Kirkersville. October 12, 1915.

Myzocallis bellus (Walsh). Jr. Ec. Ent., Vol. 10, p. 423. On black oak (*Quercus velutina*). Wooster. September 14, 1917.

Myzocallis discolor (Monell). Jr. Ec. Ent., Vol. 10, p. 423. On swamp oak (*Quercus bicolor*). Wooster. September 20, 1917.

Myzocallis punctatellus (Fitch). Jr. Ec. Ent., Vol. 10, p. 423. On chestnut (*Castanea dentata*). Wooster. September 19, 1917.

Myzocallis punctatus (Monell). Jr. Ec. Ent., Vol. 10, p. 423. On swamp oak (*Quercus bicolor*). Kirkersville. October 2, 1915.

Myzocallis tilia (Linn.). Jr. Ec. Ent., Vol. 10, p. 423. On linden (*Tilia americana*). Wooster. September 20, 1917.

Myzocallis ulmifolii (Monell). Jr. Ec. Ent., Vol. 10, p. 423. On elm (*Ulmus americana*). Wooster. September 15, 1917.

Myzocallis walshi (Monell). Jr. Ec. Ent., Vol. 10, p. 423. On hickory (*Carya glabra*). Winterset. August 11, 1916.

DREPANOSIPHINA.

Drepanaphis acerifoliae (Thomas). Bul. 826, U. S. D. A., 1920, p. 31. On maple (*Acer saccharum*). Columbus. May 14, 1916.

Drepanaphis monelli (Davis). An. Ent. Soc. Amer., Vol. 2, p. 197. On *Aesculus glabra*. Columbus. October 26, 1922. J. T. Potgieter, Coll.

Neosymydobius albasiphus (Davis). Bul. 826, U. S. D. A., p. 32. On white oak (*Quercus alba*). Winterset. August 11, 1916. Determined by J. J. Davis.

CHAITOPHORINA.

Chaitophorus viminalis Monell. Jr. Ec. Ent., Vol. 10, 1917, p. 429. On *Salix* sp. Toledo. October 11, 1917.

Periphyllus negundinis (Thomas). Bul. 826, U. S. D. A., 1920, p. 34, and Bul. 173, Ia. Agr. Exp. Sta., 1917. On box elder (*Acer negundo*). Columbus. September 3, 1916.

Neothomasia populicola (Thomas). Bul. 826, U. S. D. A., 1920, p. 35. On *Populus* sp. Winterset. August 8, 1916.

Sipha flava Forbes. Tech. Bul. 12, part 8, U. S. D. A., 1909, p. 156. On sorghum. Batavia. July 30, 1917.

PTEROCOMMINA.

Pterocomma bicolor (Oest.). Jr. Ec. Ent., Vol. 10, p. 431. On *Salix* sp. Rock Bridge. September 30, 1917. P. R. Lowry, Coll.

Pterocomma flocculosa (Weed). Jr. Ec. Ent., Vol. 10, p. 431. On *Salix nigra*. Wooster. October 22, 1917. J. S. Houser, Coll.

Pterocomma populæ (Kalt.). Jr. Ec. Ent., Vol. 10, p. 431. On *Bromus* sp. Sugar Grove. October 20, 1912. W. W. Marshall, Coll.

Pterocomma smithiæ (Monell). Jr. Ec. Ent., Vol. 10, p. 431. On *Salix alba vitellina*. Wooster. October 22, 1917. J. S. Houser, Coll.

Tribe Aphidini.

APHIDINA.

*Anuraphis*¹ *prunicola* (Kalt.). Farmers Bul. 1128, U. S. D. A., p. 28. On peach foliage. Toledo. October 11, 1917.

Anuraphis bakeri (Cowen). Farmers Bul. 1128, U. S. D. A., p. 12. On red clover. Common throughout state.

Anuraphis cardui (Linn.). Farmers Bul. 1128, U. S. D. A., p. 17. On thistle (*Cnicus lanceolatus*). Winterset. October 20, 1916.

Anuraphis crataegifolia (Fitch). Pro. Biol. Soc., Washington, Vol. 32, p. 185. On *Crataegus* sp. Sugar Grove. October 20, 1912. W. W. Marshall, Coll.

Anuraphis maidiradicis (Forbes). Seventeenth Rept. Ill., 1891, p. 64. Roots of corn. Winterset. August, 1916.

Anuraphis persicæ-niger (Smith). Farmers Bul. 1128, U. S. D. A., p. 26. Common on peach roots throughout the state.

Anuraphis roseus Baker. New name for *Aphis sorbi*. Can. Ent., Vol. 53, p. 95, and Cornell Univ. Agr. Exp. Sta. Memoir 24. On apple. Common throughout the state.

Anuraphis middletoni (Thomas). Univ. Calif. Tech. Bul., Vol. 3, No. 1, 1919, p. 115. On the roots of *Erigeron canadense*. Cedar Point. July 29, 1915.

Aphis asclepiadis Fitch. Jo. Ec. Ent., Vol. 3, p. 482. On *Asclepias* sp. Cedar Point. July, 1916.

Aphis atriplicis Linn. Univ. Calif. Tech. Bul., Vol. 3, No. 1, p. 93. On curly dock. Columbus. June 6, 1917.

Aphis carduella Walsh. Geol. and Nat. Hist. Survey of Minn. Bul. 4, p. 59. On *Cnicus lanceolatus*. Wooster. October 31, 1917.

Aphis cephalanthi Thomas. Bull. Ill. Lab. of Nat. History, Vol. 10, article 2, p. 112. On *Cephalanthus occidentalis*. Cedar Point. July 15, 1912. W. W. Marshall, Coll.

Aphis cerasifolii Fitch. Bul. 233, Me. Agr. Exp. Sta., p. 260. On choke cherry (*Prunus virginiana*). Cedar Point. August 6, 1915.

Aphis coreopsidis (Thomas). Jr. Ec. Ent., Vol. 3, p. 483. On *Bidens bipinnata*. Kirkersville. October 2, 1915.

Aphis cornifoliæ Fitch. Univ. Calif. Tech. Bul., Vol. 3, No. 1, p. 100. On cultivated sunflower. Wooster. September 19, 1917.

Aphis eupatorii Oest. Bul. 4, Geol. and Nat. Hist. Survey, Minn., p. 59. On boneset (*Eupatorium perfoliatum*). Cedar Point. August 4, 1915.

¹ The genus *Anuraphis* is now being monographed by Dr. A. C. Baker of U. S. D. A.

Aphis folsomii Davis. Jr. Ec. Ent., Vol. 3, p. 485. On Virginia creeper (*Psedera quinquefolia*). Wooster. August 2, 1917.

Aphis frondosæ Oest. Bul. 4, Geol. and Nat. Hist. Survey, Minn., p. 67. On *Bidens frondosa*. P. R. Lowry, Coll.

Aphis gossypii Glover. Bul. 257, Tex. Agr. Exp. Sta. On cultivated cucumbers throughout the state.

Aphis heraclella Davis. (N. N. for *A. heracalii* Cowen). Can. Ent., Vol. 51, p. 228. On *Cicuta maculata*. Wooster. September 13, 1917.

Aphis helianthi Monell. Jr. Ec. Ent., Vol. 3, p. 485. On sunflower (*Helianthus* sp.). Bond Hill. October 13, 1917.

Aphis illionoisensis Shimer. Jr. Ec. Ent., Vol. 3, p. 485. On cultivated grape throughout the state.

Aphis lutescens Monell. Jr. Ec. Ent., Vol. 3, p. 487. On *Asclepias* sp. Columbus. October 17, 1916.

Aphis maidis Fitch. Jr. Ec. Ent., Vol. 3, p. 487. On corn. Common throughout the state. Always above ground.

Aphis monardæ Oest. Bul. 4, Geol. and Nat. Hist. Survey, Minn., p. 58. On *Monarda* sp. Cedar Point. July 18, 1916.

Aphis oenotheræ Oest. Bul. 4. Geol. and Nat. Hist. Survey, Minn., p. 62. On chrysanthemum in greenhouse. Medina. March 28, 1918.

Aphis pomi De Geer. Memoir 24, Cornell Agr. Exp. Sta., 1919, p. 686. On apple throughout the state. Feeding on new growths.

Aphis rumicis Linn. Bul. 4. Geol. and Nat. Hist. Survey, Minn., p. 61. Common on many host plants (*Chenopodium*, *Rumex*, etc.) throughout the state.

Aphis sambuci Linn. Bul. 826, U. S. D. A., 1920, p. 43. On *Sambucus* sp. Kirkersville. October 14, 1916.

Aphis sambucifoliæ Fitch. Univ. Calif. Tech. Bul. Vol. 3, Part 1, p. 123. *Sambucus canadensis*. Wooster. September 21, 1917.

Aphis spiræphila Patch. Bull. 233, Me. Agr. Exp. Sta., p. 270. On spirea. Wooster. July 16, 1920. P. R. Lowry, Coll.

Aphis spiræcola Patch. Bul. 233, Me. Agr. Exp. Sta., p. 270. On *Spiræa Van Houtii*. Columbus. August 27, 1922. J. T. Potgieter, Coll.

Aphis vernoniæ Thomas. Jr. Ec. Ent., Vol. 3, p. 492. On *Vernonia altissima*. Winterset. August 11, 1916.

Aphis viburnicola Gill. Jr. Ec. Ent., Vol. 3, p. 492. On snowball (*Viburnum opulus*). Columbus. May 5, 1917.

Brevicoryne brassicæ (Linn.). Bul. 826, U. S. D. A., p. 45. Common throughout the state on cultivated cabbage and other cruciferous plants.

Cavariella capræ (Fab.). Univ. Calif. Tech. Bul., Vol. 3, No. 1, p. 132, and Bul. 826, U. S. D. A., p. 46. Cultivated parsnip. Kirkersville. September 15, 1919.

Cavariella pastinacea (Linn.). Univ. Calif. Tech. Bul., Vol. 3, No. 1, p. 133. On honeysuckle. Columbus. May 12, 1916.

Cerosipha rubifolii (Thomas). Jr. Ec. Ent., Vol. 3, p. 492. On blackberry. Winterset. August 18, 1915.

Hyadaphis xylostei Schrk. Bul. 826, U. S. D. A., p. 47. On honeysuckle. Columbus. May 12, 1916.

Hysteroncúra setariæ (Thomas). Can. Ent., Vol. 51, p. 228 and p. 268. On *Prunus* sp. Columbus. October 7, 1919. P. R. Lowry, Coll.

Hyalopterus arundinis Fab. Bul. 233, Me. Agr. Exp. Sta., p. 266, and Bul. 826, U. S. D. A., p. 48. On *Phragmites communis*. W. W. Marshall, Coll.

Hyalopterus atriplicis (Linn.). Jr. Ec. Ent., Vol. 5, p. 407 (*Aphis atriplicis*). On *Chenopodium alba*. London. July 25, 1922. J. T. Potgieter, Coll.

Liosomaphis berberidis (Kalt.). Univ. Calif. Tech. Bul., Vol. 3, p. 130. On *Berberis serotina*. Wooster. November 17, 1917. Scott Harry, Coll.

Rhopalosiphum hippophoes Koch. Univ. Calif. Tech. Bul. Vol. 3, p. 81. On cultivated buckwheat. Wooster. September 12, 1917.

Rhopalosiphum nymphaeæ (Linn.). Bul. 826, U. S. D. A., p. 49. On water lily (*Castalia tuberosa*). Columbus. October 17, 1916.

Rhopalosiphum prunifoliae (Fitch)—“Apple-grain aphid.” Memoir 24, Cornell Agr. Exp. Sta. Common on apple and grass throughout the state.

Rhopalosiphum pseudobrassicæ (Davis) — (*Aphis pseudobrassicæ* Davis). Can. Ent., Vol. 46, p. 231. On cultivated turnips. Wooster. October 29, 1917.

Rhopalosiphum rhois Monell. Univ. Calif. Tech. Bul., Vol. 3, p. 86. On *Rhus typhina*. W. W. Marshall, Coll.

Rhopalosiphum rufomaculata (Wilson). An. Ent. Soc. Amer., Vol. 3, p. 323. (*Coloradoa rufomaculata*). On chrysanthemum in greenhouse. Columbus. March 8, 1917.

MACROSIPHNA.

*Amphorophora*¹ *crataegi* (Monell). U. S. Geol. and Geo. Survey Bull., Vol. V, p. 20. (*Siphonophora crataegi*) on *Crataegus* sp. Wooster. August 2, 1920. P. R. Lowry, Coll.

Amphorophora nabali (Oest.). Geol. Survey Minn., 14 Report, p. 34, 1886, (*Rhopalosiphum nabali*). On *Prenanthes trifoliolata*. Sugar Grove. October 4, 1919.

Amphorophora rubicola (Oest.). Geol. and Nat. Hist. Survey of Minn., 14 Report, p. 27 (*Macrosiphum rubicola*). On black raspberry. Cedar Point. July 15, 1915.

Amphorophora rubi (Kalt.). Kaltenbach, 1843. Mon. der Pflanzenlause, p. 24. (*Aphis rubi*). Black raspberry. Dover. July 17, 1922. F. F. Smith, Coll.

¹ Species of the genus *Amphorophora* were identified by Mr. P. W. Mason, U. S. D. A., who is now monographing the genus.

Capitophorus tetrarhodus Walker. Hollandischen Blattlause. P. Van der Goot, p. 128, and Bul. 233, Me. Agr. Exp. Sta., p. 269 (*Myzus rosarum*). On rose. Wooster. October, 1917.

Illinoia liriodendri (Monell). Bul. 826, U. S. D. A., p. 56. On tulip tree (*Liriodendron tulipifera*). Wooster. September 20, 1917.

Illinoia pisi (Kalt.). Univ. Calif. Tech. Bul., Vol. 3, p. 66 (*Macrosiphum pisi*). Common on peas and clover throughout the state.

Macrosiphoniella sanborni (Gill). Mem. Ind. Mus., Vol. 6, p. 164, and Can. Ent., Vol. 50, p. 65. On chrysanthemum in greenhouse. Columbus. January 6, 1917.

Macrosiphum erigeronensis (Thomas). Bul. 282, Me. Agr. Exp. Sta., p. 218, and Aphididæ of Neb., p. 76. On *Erigeron canadense*. Cedar Point. July 6, 1914. W. W. Marshall, Coll.

Macrosiphum eupatorii (Williams). Aphididæ of Neb., Williams, p. 77. On *Eupatorium perfoliatum*. Wooster. September 13, 1917.

Macrosiphum gauræ (Williams). Aphididæ of Neb., Williams, p. 79. On carnation. Columbus. November 2, 1916.

Macrosiphum granarium (Kirby). Jr. Agr. Research, Vol. 7, p. 463. On cultivated oats. Winterset. June 29, 1915.

Macrosiphum lactuca (Kalt.). Univ. of Calif. Tech. Bul., Vol. 3, p. 65. On lettuce in greenhouse. Columbus. March 6, 1918. P. R. Lowry, Coll.

Macrosiphum luteola (Williams). Bul. 282, Me. Agr. Exp. Sta., p. 218, and Aphididæ of Neb., Williams, p. 82. On *Ambrosia artemisiæ-folia*. Winterset. August 20, 1915.

Macrosiphum rosea (Linn.). Bul. 282, Me. Agr. Exp. Sta. Common throughout the state on rose.

Macrosiphum rudbeckiæ (Fitch). Univ. Calif. Tech. Bul., Vol. 3, p. 67. On golden glow (*Rudbeckia laciniata*). Common throughout the state.

Macrosiphum solanifolii Ash. Bul. 27, Va. Truck Exp. Sta., 1919. Common throughout the state on a variety of host plants. "Pink and green potato aphid."

Macrosiphum taraxaci (Kalt.). Univ. Calif. Tech. Bul., Vol. 3, p. 71, and Bul. 282, Me. Agr. Exp. Sta., p. 218. Common on dandelion.

Macrosiphum vernaefusca Davis. Can. Ent., Vol. 46, p. 77. On *Rumex acetosa*. Wooster. September 15, 1917.

Myzus cerasi (Fab.). Bul. 233, Me. Agr. Exp. Sta., p. 258. On cherry. Common throughout the state.

Myzus circumflexus (Buckton). Univ. Calif. Tech. Bul., Vol. 3, p. 74. On Easter lily in greenhouse. Medina. February 21, 1918.

Myzus houstonensis (Troop). Farm. Bul., U. S. D. A. 1128, p. 34. On cultivated gooseberry. Columbus. June, 1923. D. M. DeLong, Coll.

Myzus persicæ (Sulz.). Univ. Calif., Tech. Bull., Vol. 3, p. 85. Found on many host plants. Common throughout the state. "The green peach aphid."

Myzus plantagineus Pass. Jr. Ec. Ent., Vol. 3, p. 495. On *Plantago major*. Winterset. August 2, 1916.

Myzus ribis (Linn.). Bul. 225, Me. Agr. Exp. Sta., p. 55. On cultivated currant. Winterset. October 20, 1916.

Phorodon humuli (Schr.). Univ. Calif. Tech. Bul., Vol. 3, p. 79. On plum. Winterset. September 13, 1915.

Subfamily ERIOSOMATINÆ.

Tribe Eriosomatini.

Eriosoma americana (Riley). Univ. Calif., Tech. Bul., Vol. 3, p. 148. On *Ulmus americana*. Wooster. July 14, 1920. P. R. Lowry, Coll.

Eriosoma crataegi (Oest.). Bul. 4, Geol. and Nat. Hist. Survey, Minn., p. 27. On *crataegus*. Wooster. July 14, 1920. P. R. Lowry, Coll.

Eriosoma lanigerum (Hausm.). Univ. Calif., Tech. Bul., Vol. 3, p. 149. On apple and elm. Common throughout the state.

Eriosoma rileyi (Thomas). U. S. D. A. Report 101, 1915, p. 15. On *Ulmus americana*. July 27, 1920. P. R. Lowry, Coll.

Colopha umicola (Fitch). Univ. Calif., Tech. Bul., Vol. 3, p. 148. On elm. Common throughout the state.

Gobaishia ulmifusus (Walsh). Bul. 181, Me. Agr. Exp. Sta., p. 220. (*Pemphigus ulmifusus*). Slippery elm. Cleveland. July 6, 1920. J. P. Sobey, Coll.

Tribe Pemphigini.

Mordwilkoja vagabunda (Walsh). An. Ent. Soc. Amer., Vol. 7, p. 67. On *Populus deltoides*. Cedar Point. June 20, 1915.

Pemphigus burserus (Linn.). Arkiv. for Zoologi, Band 5, No. 14, p. 114, and Bul. 213, Me. Agr. Exp. Sta., p. 78. On *Populus deltoides*. Put-in-Bay. L. L. Huber, Coll.

Pemphigus populi-transversus Riley. Jr. Agr. Research, Vol. 14, p. 577. On *Populus deltoides* and roots of *Barbarea vulgaris*. Columbus. 1917.

Tribe Melaphini.

Melaphis rhois (Fitch). Bul. 826, U. S. D. A., 1920, p. 74. On sumac. Sugar Grove. September 1, 1903. H. Osborn, Coll.

Tribe Prociphilini.

Neoprociphilus attenuatus (O. and S.). Bul. 202, Me. Agr. Exp. Sta., p. 174. Reported as common on *Similax rotundifolia* in Ohio by Jackson.¹

Prociphilus fraxinifolii (Riley). Bul. 5, U. S. Geol. and Geog. Survey Terr., p. 17, and Bul. 270, Me. Agr. Exp. Sta. On *Fraxinus americana*. Cedar Point. July 6, 1915.

Prociphilus imbricator (Fitch). Proc. Columbus Hort. Soc., Vol. 22, p. 188, and Bul. 270, Me. Agr. Exp. Sta. On beech (*Fagus grandifolia*). Wooster. September 24, 1917.

¹ Proceedings Columbus Horticultural Society, Vol. 22, p. 214.

Prociphilus tessellata (Fitch). Proc. Columbus Hort. Soc., Vol. 22, p. 183, and Bul. 270, Me. Agr. Exp. Sta. On *Alnus*. Common throughout the state.

Thecabius populi-conduplicifolius (Cowen). An. Ent. Soc. Amer., Vol. 7, p. 61. On *Populus candicans*. Wooster. July 19, 1920. P. R. Lowry, Coll.

Tribe *Fordini*.

Forda olivacea Rohr.? Psyche, Vol. 15, p. 68. In ants nest. Delaware. May 5, 1920. P. R. Lowry, Coll.

Geoica squamosa Hart. Bul. 826, U. S. D. A., p. 79. On wheat roots. New Stark. June 8, 1923. W. G. Stover, Coll.

Subfamily HORMAPHIDINÆ.

Tribe *Hormaphidini*.

Hamamelistes spinosus Shimer, and *Hormaphis hamemelidis* Fitch. Tech. Series Bul. 9, U. S. D. A. Neither of these species have been taken in Ohio, but are quite likely to occur wherever witch-hazel and birch are found. Common in border counties of Pennsylvania.

Tribe *Cerataphidini*.

Cerataphis lataniæ (Licht.). Bul. 826, U. S. D. A., p. 87. On palm (*Pritchardia filifera*) in greenhouse. J. G. Sanders, Coll.

Subfamily PHYLLOXERINÆ.

Tribe *Phylloxerini*.

Phylloxera caryaecaulis Fitch. Proc. Davenport Ac. Sci., Vol. 9, p. 244. On hickory. Worthington. May 31, 1920. P. R. Lowry, Coll.

Phylloxera caryaevenæ Fitch. Proc. Davenport Ac. Sci., Vol. 9, p. 239. On hickory. Worthington. May 31, 1920. P. R. Lowry, Coll.

Phylloxera picta Perg. Proc. Dav. Ac. Sci., Vol. 9, p. 197. On hickory. Wooster. July 4, 1920. P. R. Lowry, Coll.

Phylloxera popularia Perg. Proc. Dav. Ac. Sci., Vol. 9, p. 266. In galls of *Pemphigus populi-transversus* on *Populus* sp. Sandusky. September 10, 1920. P. R. Lowry, Coll.

Phylloxera vitifolia (Fitch). Bul. 903, U. S. D. A., 1921. On wild grape. Cedar Point. July 17, 1912. W. W. Marshall, Coll.

Tribe *Chermesini*.

Chermes pinicorticis (Fitch). Bul. 173, Me. Agr. Exp. Sta., p. 303. On *Pinus strobus*. Columbus. April 15, 1920.

ECOLOGY.

Aphididæ show very definite relations to the factors of environment. These relations will be discussed under separate factors.

Edaphic Factors.

The structure temperature, water content, and probably the chemical composition of the soil has a direct bearing upon the presence or absence of certain root-feeding forms of Aphididæ. The more open types of soil are, for the most part, more favorable to the growth and multiplication of root-feeding aphids. In a planting of young peach trees on a hillside the absence of root-feeding form of *Anuraphis persicæ-niger* was noticed in heavy clay soil of the orchard, while all the trees in a gravelly clay soil were infested with the species. In California the type of soil favorable to the growth and reproduction of the grape phylloxera (*Phylloxera vitifoliæ*) seems to be somewhat different.

Davidson and Nougaret¹ found that vines growing in heavy soils, more or less shallow, with compact clay subsoils, die out much sooner from the attack of the aphids than vines growing in well drained soils; that vines growing in very loose friable sandy soil, or one with a surface blow of sand several inches deep, seemed to be almost immune to the attack of the phylloxera.

Soil moisture definitely controls the rate of reproduction of the sugar-beet root-louse (*Pemphigus betæ* Doane). Parker² found in both field and laboratory experiments that the greater the moisture content of the surface soil the lower the rate of reproduction, and that migrating forms of the plant louse from *Populus* species showed a very decided preference for beet plants growing where the surface soil was dry.

Soil further determines the absence or presence of the Aphididæ by the influence exerted on the distribution and growth of the host plants.

Climatic Factors.

Temperature: Temperature has an extensive influence on the metabolism and reproduction of the Aphididæ. The time of hatching of the over-wintering eggs is determined by the

¹ Bul. 903, U. S. D. A., 1921, p. 16.

² Jr. Agr. Research, Vol. 4, p. 241-250.

early spring temperature. The growth and development of all forms are dependent upon temperature. The temperature factor is probably most marked in the development of the early spring generations in Ohio. Ewing¹ found that *Aphis avenæ* (*Rhopalosiphum prunifoliæ*) has its optimum development at a temperature of sixty-five degrees F., and that at ninety degrees F. development stopped. Headlee² found that a range in relative humidity of from thirty-seven to complete saturation had little effect on the development of *Toxoptera graminum* at a temperature of eighty degrees F.

Temperature change has an influence on the life cycle of Aphididæ. *Macrosiphum solanifolii* in Ohio begins the spring generation by the hatching of the stem mothers from the over-wintering eggs on rose. There follows viviparous parthenogenetic generations on rose and later on plants of the Solanum family, and with the coming of cold weather there is a return migration to the rose where the oviparous generation is produced and the over-wintering eggs are laid. Smith³ has shown that in the coastal plains region south of Chesapeake Bay, Virginia, the oviparous forms are not known, but that the insect passes the mild winter as parthenogenetic, viviparous females. Gillette and Thomas⁴ have shown that *Pemphigus populi-transversus* in its alternation from Populus to roots of cruciferous plants has a different behavior in the south than in the north. In the north the "true sex" forms are found in the fall and over-wintering eggs are laid, while in the south the "true sex" forms do not appear until spring and the eggs hatch soon after oviposition.

Air Movements: Air movements serve as a very important means of dispersal of all flying Aphididæ. Migrating forms carried by the wind are frequently noticed, especially in certain parts of the day. This means of dispersal adds greatly to the success of the species in that new host plants are found and some natural enemies are left behind. In a large field planted to peas which became heavily infested with the pea aphid (*Illinoia pisi*) the eastern part of the field seemed to be the more recent point of infestation. This seemed evident from

¹ Biological Bulletin, Vol. 31, p. 53.

² Jr. Ec. Ent., Vol. 7, p. 416.

³ Bul. 27, Va. Truck Exp. Sta., 1919.

⁴ Jr. Agr. Research, Vol. 14, p. 577-593.

the fact that in the western part of the field the pea plants were entirely killed and the ground was covered with many dead aphids, while in the eastern part the pea plants were not entirely dead, and contained many living aphids. The afternoon and evening breezes of the locality are mostly from the west.

Air Moisture: Peterson¹ found that air of high moisture content is more favorable to the hatching of the eggs of *Aphis avenæ* (*Rhopalosiphum prunifolium*) than air of low moisture content. Hot dry winds are supposed to kill many Aphididæ.

Biotic Factors.

Food Relation: The food supply of Aphididæ has a definite effect upon the structure of the individuals. With a given host plant, in thrifty growing condition, the tendency in reproduction is to produce apterous forms only, but with drying up of the host plant the production of winged forms is the rule. It seems quite probable to the writer that the production of the "true sex" forms may be in a measure a response to a seasonal condition of the host plant.

Pergande² in his work with *Hormaphis hamamelidis* Fitch and *Hamamelistes spinosus* Shimmer showed these two species to have a most remarkable change of form associated with a change of habitat and food plants. The stem mothers and migrants from witch-hazel to the birch are of the ordinary aphid type. The first generation on the birch develop into aleurodian-like forms which in turn give rise to two more like generations. The last aleurodid-like form produces the return sexupare to the witch-hazel which are of the aphid type. Galls are produced on the witch-hazel by these species while no such growths are formed on the birch. The writer has not verified the life histories as given by Pergande, but has taken the various stages of the insects on witch-hazel and birch in several localities.

Association of Species.

It has long been known that in every aphid colony there is an association of other insects bearing a very definite relation to the plant lice. These insects may exist as predators, parasites, symbionts or guests of the species. The relation of the

¹ Bul. 332, N. J. Agr. Exp. Sta.

² Tech. Bul. 9, U. S. D. A.

symbionts may be somewhat complex as will be pointed out for ants of certain species in their relation to the *species Anuraphis maidiradicis* in its under-ground existence. Certain species of the families Tabanidæ and Muscidæ, species of *Bombus*, *Apis mellifera* Linn., together with the ants are attracted to the colonies by the presence of the sweetish excrement characteristic of many species of the Aphididæ. The predators and parasites add to the complexity of the community by introducing their parasites and hyperparasites. The following lists of species found associated in aphid colonies will give something of the complex.

In observations made on an association of insects acting as predators or parasites in colonies of *Macrosiphum solanifolii* the following species were reported by Houser, Guyton and Lowry:¹

Predators—

Nine species of Coccinellidæ larvæ and adults as follows:

<i>Hippodamia convergens</i> Guer.,	<i>Coccinella 9-notata</i> Hebst.,
<i>Hippodamia glacialis</i> Fabr.,	<i>Coccinella sanguinea</i> Linn.,
<i>Hippodamia parenthesis</i> Say,	<i>Megilla maculata</i> De Geer,
<i>Hippodamia 13-punctata</i> Linn.,	<i>Brachyacantha ursina</i> Fab.,
<i>Adalia bipunctata</i> Linn.	

Three species of Syrphidæ larvæ as follows:

<i>Syrphus americanus</i> Wied.,	<i>Allograpta obliqua</i> Say,
<i>Sphaerophoria cylindrica</i> Say.	

Larvæ of *Chrysopa* sp. were also predators.

Parasites—

Aphidius polygonaphis Fitch, *Pachyneuron aphidivorum* Ashm.

Two species of *Lygocerus*.

Diplazon laetatorius Fabr. and *Pachyneuron texanus* Gir.

The last two of the parasites named are parasites of the larvæ of syrphus flies.

Associated with this insect association were the following birds which acted as predators upon the insects:

Chipping sparrow (*Spizella passerina passerina* Bechstein), quail (*Colinus virginianus virginianus* Linn), English sparrow (*Passer domesticus* Linn), and the common fowl (*Gallus domesticus*).

It is undoubtedly true that many other species enter into the association, but the foregoing list is enough to show some-

¹ Bull. 317, Ohio Agr. Exp. Sta.

thing of the species which seem dependent upon conditions favorable to the growth and increase of *Macrosiphum solani-folii*, which in turn for best development depends upon plant growth and the comparative absence of its enemies.

Again much the same was noted in an outbreak of *Illinoia pisi* in a pea field in which all the pea plants are practically destroyed. Dead larvæ of Coccinellidæ, Syrphidæ and Chrysophidæ were common on the ground; and cases were common of cannibalism among like species. It seemed evident that the existence of the association, as such, depended upon the ability of the pea plants to keep living and produce a succulent growth for the maintenance of the aphid colonies, at least, one can safely say that the death of the pea plants hastened the breaking up of the intensity of the association, resulting in a more nearly normal number of species. The following list of species were taken in this field, the numerals after the species name are indicative of the proportion of occurrence:

The predaceous larvæ and adult forms of *Hippodamia parenthesis* Say (4), *Hippodamia 13-punctata* Linn. (1), *Hippodamia convergens* Guer (3), *Adalia bipunctata* Linn. (5), *Coccinella sanguinea* Linn. (2), *Coccinella 9-notata* Hebst. (2), *Coccinella transversoguttata* Fabr. (6).

The predaceous larvæ of *Syrphus ribesii* L. var. *vittafrons* Shan (5), *Syrphus rectus* O. S. (3), *Allograpta obliqua* Say (2), and the adult ground beetle *Lebia atriventris* Say (1).

The following Diptera were present in the association: *Leucopis nigricornis* Egger (6), a species reported as predaceous in the larval form on aphids.¹ *Distichona varia* V. d. W. was also taken, but its relation in the association was not determined.

The following Hymenopterous parasites were in much evidence in the association. The relative numbers of the species were not determined, but results of their activity were much in evidence: *Syrphoctonus agilis* Cress., *Aphidius rosæ* Hal., *Megorismus fletcheri* Cwfd., *Pachyneuron* sp., *Praon simulans* Prov., *Perilampus chrysopæ* and *Lygocerus* sp.

Of the above *Aphidius rosæ*, *Megorismus fletcheri* and *Praon simulans* are reported as parasites of aphids; and certain species of the genus *Pachyneuron* are also aphid feeders. Species of the genus *Parilampus* are reported as feeding on *Comiplex*

¹ New Series Bul. 10, U. S. D. A., p. 76.

fugitives, another species of Hymenoptera; as is a species of the genus *Pachyneuron* on *Diplazon* sp.

The following observation was made in an apple orchard April 9, 1919, between the hours of two and three P. M.

The day was clear and somewhat warm for that time of the year. Large numbers of the eggs of *Rhopalosiphum prunifolium* were hatched and the young migrated to the developing apple buds which were nearly ready to begin sending out leaflets. Something of the number may be gained from the count made of fifty-seven buds which contained 3,920 young aphids, or an average of nearly seventy to each bud. The following species were taken in or near the colonies, and in their larval or larval and adult stages are known to be predators of the Aphididæ.

Lady beetles were present in about the proportion of the numerals which follow the species name.

Coccinella 9-notata Hebst. (7), *Adalia bipunctata* Linn. (2), *Hippodamia parenthesis* Say (1), and *Coccinella sanguinea* Linn. (1).

Syrphus flies were represented by a single species, *Syrphus torvus* O. S., which was present on an average of six to each tree.

A species of saw fly of the genus *Selandria* was seen going over the colonies, but its relation was not determined.

From these brief studies a hint of the vast complex which exists in an association dependent upon the aphid colony becomes evident. Under average conditions of plant louse production a balance would be struck in which the activity of the host, predaceous forms, parasites and hyperparasites would tend to be equal. In the case cited of the pea field, it is evident that biotic and weather conditions were such that *Illinoia pisi* grew and increased quite rapidly. Toward the end of such a period of temporary success of a species the number of individuals in the association is greatly increased and the interdependence of the associated species magnified. The association in a particular plant group would tend to be much the same at all times and is only temporarily dominated by a particular species.

In so far as the writer knows there seems to be but few instances where aphid species are interdependent. *Phylloxera popularia* Perg. is found only in the galls formed by the genus *Pemphigus* and probably the existence of the species now depends upon the presence or absence of the *Pemphigan* galls.

There are many instances where it seems that aphids are dependent upon species of ants for success. The best known is probably the relation between *Anuraphis maidiradicis* and various ants, especially the corn field ant (*Lasius niger* L.). The ants collect the eggs of the plant lice in the fall and carry them down below the frost line in the ant's nest. With the coming of spring the young aphids are brought up to the roots of various grasses and weeds, and cared for by the ants. Many observers have noticed the ants carrying the aphids from corn plant to corn plant through the growing season, thus establishing new colonies. It seems likely that this relation has existed so long that the completion of the aphid's life cycle is dependent upon the ant's care.

Seasonal Succession.

The migration of Aphididæ from host to host seems to follow some seasonal change in the host plant. There are many instances of species spending the winter and the early part of the growing season on one host and then migrating for a period to one or many hosts, deserting entirely the primary host species. Later in the season there is a return migration from the secondary hosts to the primary host, where the "true sex" forms produce the fertilized, over-wintering egg. A good illustration of this is found in the behavior of *Anoecia corni*. The over-wintering and spring host is *Cornus* species, and the summer host is the grasses, especially orchard grass (*Dactylis glomerata*). The return migration in this species is rather late in the fall, taking place about the last week in October in the vicinity of Harrisburg, Pennsylvania.

At times the migration is not sharply defined; extending over a rather long period. Baker and Turner¹ pointed out an example of this in *Rhopalosiphum prunifolium* in its migration from and to the apple. In extreme cases the return migration is not complete, as in the case of the fall migration of *Eriosoma lanigerum* from apple to the elm. Here immature forms remain on the apple through the winter.

Ecological Succession.

With the change of plant covering of a given area there would come a change in the aphid population. The most

¹ Jt. Agr. Research, Vol. 18, p. 311.

important fact to support this statement is the very narrow limits of choice of host plants among the Aphididæ. With the passing of these host plants from an association the aphid species inhabiting such plants would follow the plants. Today are found certain groups of plant lice which are more or less restricted to particular groups of plants; as, for example, the tribe Lachnini, which for the most part is found on Pinaceæ, and the tribe Phylloxerini found for the most part on *Carya* species. With sufficient data of collections it seems probable that a given area might be plotted as to aphid species. At present we are undoubtedly safe in using the plant covering as an index to the species one might expect to find in a particular region.

ECONOMIC IMPORTANCE OF THE FAMILY APHIDIDÆ.

Species of the family Aphididæ occupy a major rank among economic insects. The loss in this country due to the attack of the spring grain aphid (*Taxoptera graminum*) for one year was estimated at from twelve to fifteen million dollars.¹ Plants are damaged by the loss of plant juices upon which the insect feeds through its sucking mouth parts.

Under favorable conditions the rate of increase among plant lice is very rapid. One producing female of *Macrosiphum solanifolii* was shown to be the parent of seventy-two individuals in twelve days, at which time five females were producing young.² Because of this rapid rate of reproduction a species may do very great harm in a very short period of time.

Still another mode of loss has been shown by proving the carrying of plant diseases from plant to plant by the feeding plant lice.³

Not only is there a loss occasioned by the direct attack of the species, but the cost of control measures amount to a large sum each year.

Of the list of Ohio species fifty-five species are known to be of economic importance in their attack on cultivated crops, and shade and forest trees.

¹ Webster, F. M., Am. Ent. Soc. of Amer., Vol. 2, p. 70.

² Bul. 317, Ohio Agr. Exp. Sta., p. 65.

³ Science, Vol. 50, p. 342.

Bul. 297, Me. Agr. Exp. Sta.

Jr. Agr. Research, Vol. 21, No. 1.

Bul. 303, Me. Agr. Exp. Sta., p. 340-343.

Aphids as Fruit Pests.

Aphididæ rank among the major insect pests of apple. The rosy aphid (*Anuraphis roseus*) stands first, injuring both fruit and foliage. This species may be especially harmful in the northern part of Ohio. The green apple aphid (*Aphis pomi*) is second of the species in rank attacking apple. This species attacks the newer growths, and is especially harmful to young trees. The wooly apple aphid (*Eriosoma lanigerum*) does a damage which is somewhat difficult to estimate, attacking the tree both above and below ground. Several other species may be found on apple. The apple-grain aphid (*Rhopalosiphum prunifolium*) is quite numerous on the apple in the fall and early spring, but probably does a minor injury. At times the green apple aphid (*Aphis pomi*) may do some damage to quince.

Young peach trees are frequently killed by an attack of the black peach aphid (*Anuraphis persicæ-niger*) on the roots. The writer's attention was called to a planting of four thousand trees of which one-fourth had been killed by the insect. The green peach aphid (*Myzus persicæ*) may at times do considerable damage to the foliage of the peach.

The foliage of the cultivated cherry is deformed into gall-like masses by the feeding of the black cherry aphid (*Myzus cerasi*). The damage done each year by this species is considerable. Plums are attacked by several species. The rusty plum aphid (*Hystroneura setariæ*) severely injures Japanese varieties, especially in the South. *Anuraphis cardui*, *Rhopalosiphum nymphaeæ*, *Phorodon humuli* and *Hyalopterus arundinis* may at times injure the foliage of plum.

Aphididæ in Relation to Grain Crop Production.

The wheat crop of this country, especially in the south and southwest in certain years, is threatened with total loss by the ravages of the spring grain aphid (*Toxoptera graminum*). As before mentioned, the loss to wheat in 1907 was estimated at twelve to fifteen million dollars. It is quite probable that this species is a controlling factor in the extension of the wheat belt southward. This species seem to be growing in destructiveness.

The corn root aphid (*Anuraphis maidiradicis*) ranks high as a pest of corn throughout the great corn belt of this country. The species seems to be generally present, and in sections where corn is followed by corn in the crop rotation may reduce the

yield as much as fifty to seventy-five percent. Corn and wheat as well as the other grain crops are injured by several other species, both as root feeders and blade and stem feeders. *Rhopalosiphum prunifolium*, the apple grain aphid, spends the greater part of the growing season in grasses. The writer has seen this species doing a considerable damage to young wheat in the fall before migrating to the apple. *Macrosiphum granarium* lives on a large number of the grasses and is rather common in the wheat fields of Ohio, but at present seems to be of minor importance as a grain pest. *Aphis maidis* at times does an injury to corn tops and may be quite serious in sweet corn plantings. No definite estimate may be made of the injury occasioned by several grass-feeding species, but they undoubtedly greatly reduce the yield in pastures and meadows.

Aphids Attacking Truck Crops.

Two plant lice stand out as major pests in two truck crops, either of which may if unchecked bring about a total destruction of the crop they attack. The pink and green potato aphid (*Macrosiphum solanifolii*) in 1917 killed out many potato fields in Ohio, especially was the destruction marked in the southwestern section of the state. This species has a very long list of host plants among which are potato, tomato, egg plant, pepper, and spinach. The establishing of the relation of this species to the spread of plant diseases make it of still greater economic importance.¹ The other of these two is the cucumber aphid (*Aphis gossypii*). Melon and cucumber growers suffer a very heavy loss from this species. Oftentimes the vines are killed outright just at the time when they should be producing their heaviest crop. *Aphis gossypii* does not feed on such an extended number of hosts as *Macrosiphum solanifolii*.

Cruciferous plants are attacked by the cabbage aphid (*Brevicoryne brassicae*), and the false cabbage aphid (*Rhopalosiphum pseudobrassicae*). These species become especially abundant on late plantings of cabbage, radish, and turnips. *Myzus persicae* attacks a large number of truck crops, and may be especially harmful to potato plants. Several other species are found in the truck garden. The pea aphid (*Illinoia pisi*) in certain seasons may bring about a total destruction of pea plantings, and *Aphis rumicis* may at times be an important bean pest.

¹ Science, Vol. 56, p. 342.

Species of Aphids Attacking Small Fruits.

Blackberries and raspberries are hosts to a few species of plant lice. *Cerosipha rubifolii* causes a gall like twisting of the leaves of blackberry. P. C. Mason of the United States Department of Agriculture, in a private communication, reports three species of *Amphorophora* on raspberry. The writer has seen cultivated raspberries severely damaged by one of these species.

Several species of aphid play an important part in the growing of currants and gooseberries. *Myzus ribis* may cause a very heavy loss to currants by attacking the leaves, causing them to cup and curl, and to become characteristic reddish color. These leaves may fall and cause the fruit to be of poor quality. This species at times attacks the gooseberry. Of the other species found on these host plants *Amphorophora lactuæ* is probably most important. The Houghton gooseberry aphid may do considerable harm to the Houghton gooseberry, but does not seem to attack other of the *Ribes*.

Grapes are attacked by two species of aphids. The grape phylloxera (*Phylloxera vitifoliæ*) stands out as one of the most important insect pests of the grape, and it was this species that at one time threatened the grape growing industry of France, killing out two million acres of grapes before a control was discovered. Our native grapes seem to be more or less immune to its attack, but introduced varieties grown on the western coast suffer a very heavy loss each year from the attacks of this species. *Aphis illinoiensis* may at times do some damage to young grape vines by feeding upon and stunting the growth of the young arms.

The strawberry root louse (*Aphis forbesi* Weed) was described from Ohio, and is reported as quite injurious to strawberry plantings.

Aphid Species Attacking Shade and Forest Trees.

Probably less havoc is done to shade and forest trees by Aphididæ than to any other group of plants. The chermes attacking evergreens and phylloxera attacking deciduous trees, especially *Carya* species probably are the outstanding aphid pests of the forest. The elm serves as host to a number of species, several of which cause galls to form on the leaves. Species of maple when used as shade trees are at times over-run

by a number of species which may cause the foliage to become unsightly, and even drop in early summer. The number of species found on forest trees is very large.

Greenhouse Crops Injured by Aphids.

Many aphids found on plants outside may at times do injury to plants under glass. The chrysanthemum grower is quite sure to have trouble with a number of species. Roses, snapdragons, palms, ferns, lettuce, and cucumbers are at times severely infested when grown in greenhouses.

Control of Aphid Pests.

Natural Controls: Biotic enemies and adverse weather conditions make up the natural controls of the Aphididæ. Insects both as parasites and predators, several species of birds, and entomogonus fungi are chief of the biotic enemies. Extremes of heat or cold at a particular season of the year, and heavy rains kill off large numbers of Aphids.

Cultural Practices in Control of Aphids: Crop rotation will do much in control of certain aphid pests. The growing of plants which do not serve as host to the depredating species will tend to clean up the infestation. The destruction of weeds which serve as host to the species will reduce the numbers and help to prevent spread of the species to neighboring crops. Crop remnants should be destroyed soon after harvest to prevent migration from such material to growing crops. Thorough cultivation will break up the nests of aphid-attending ants, and thus protect the crop from root feeding forms.

Artificial Control Measures: Most effective of the artificial control measures for Aphididæ is the use of nicotine, preferable as a sulphate salt carried to the plant either in a dust or in a water solution. Oil emulsions may be used, but greater skill is required in preparing the spray and making the application than with the nicotine.

In greenhouses fumigation with hydrocyanic acid gas or with fumes of nicotine is successful as aphid control.

Recently attention has been directed toward the destruction of intermediate hosts. (See Bulletin 303, Maine Agricultural Experiment Station, 1921). This method is of much value where but one over-wintering host is known for a destructive aphid species. Further development depends upon a more thorough study of the life cycles of economic species.

Received for publication, May 16, 1923.

CATALOGUE OF TYPE FOSSILS IN THE GEOLOGICAL MUSEUM AT THE OHIO STATE UNIVERSITY.

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INTRODUCTION.

The following catalogue consists of an alphabetic list of all fossil types (holotypes, paratypes, and cotypes), all subsequently described and figured specimens (plesiotypes), as well as artificial models of type fossils (plastotypes) in the Geological Museum of The Ohio State University. It is patterned directly after the catalogue compiled by Dr. Charles Schuchert, assisted by W. H. Dall, T. W. Stanton, and R. S. Bassler, for the fossil invertebrates in the United States National Museum.¹

The catalogue is designed for the convenience of workers in Paleontology and in response to a constant inquiry for information concerning type specimens of Ohio fossils. Unfortunately, many of the type fossils thought to be located here, according to statements in the older reports of the Geological Survey of Ohio, are missing, and although some of them may have been lost at some former time, it seems probable that many have never been placed in this Museum, but have found their way into other collections. An attempt is now being made to recover as many as possible of the types which have been described in the reports of the Geological Survey of Ohio, and any information concerning the location of such specimens will be appreciated.

The work of collecting the data for the following catalogue of type fossils extended over a period of several years during which the writer has been engaged in identifying and reclassifying the paleontological material in the Geological Museum at The Ohio State University. The writer wishes to acknowledge her indebtedness to Dr. J. Ernest Carman, curator of the Museum, under whose direction the work was carried on, for his kind advice and for the many helpful suggestions which he has given her.

¹ Schuchert, U. S. Nat. Mus., Bull. 53, Pt. 1, 1905.

The following data is given concerning each entry in the catalogue: (1) catalogue number; (2) name of form as described or figured; (3) kind of type with number of specimens included in the entry;¹ (4) formation and locality; (5) reference to author and place of publication with additional synonymy where the type specimen has subsequently been described and figured; (6) citation of the present name if different from the original name, or cross-references where the species appears under more than one name in the catalogue. The name of the author is placed in parenthesis when the same generic name is not used as that under which it was originally described.

The definitions of terms applied to type fossils are the same in the present work as those employed by Dr. Charles Schuchert in his catalogue of type specimens of fossil invertebrates in the United States National Museum.² The following terms are used:

Primary Types or Proterotypes.

Holotype.—A single specimen selected from the original material as the type of a species, or a single specimen upon which a species is based is known as the holotype.

Paratype.—If a holotype has been selected, but if other specimens are also mentioned, described, figured, or in any way aid in the original description, the latter are called paratypes. A species may therefore have both holotype and one or more paratypes.

Cotypes.—If no holotype is selected from the original material, and if two or more specimens are used in describing and figuring a species, these types are known as cotypes.

Chirotype.—Chirotype is the term applied to material described in manuscript form. After the manuscript has been published the chirotype will become either a holotype, paratype, etc.³

¹ When more than one specimen is included in a single entry, as is often the case in cotypes, plesiotypes, etc., the number of specimens is given in parenthesis after the kind of type. Thus there are many more individual type specimens than there are entries in the catalogue.

² Schuchert, U. S. Nat. Mus., Bull. 53, Pt. 1, 1905, pp. 9-15.

³ In this catalogue chirotypes have been marked whenever possible by placing after the prefix "Chiro" (manuscript) the kind of type which the material will become after the publication of the manuscript, as *Chiroholotype*, *Chiroparatype*, etc. In cases, however, in which the investigation has not progressed far enough to designate a specimen as chiroholotype, chirocotype, etc., only the term *Chirotype* is used. Likewise in such instances no catalogue number has yet been assigned.

Secondary or Supplementary Types.

Plesiotype.—A specimen from any locality which is compared with a species already established, and which is described and figured as such, is called a plesiotype.

Artificial Models.

Plastotype.—An artificial cast or model made directly from a primary type is called a plastotype.

Figured Specimens.

A number of specimens are included which cannot be classed as real types, but which have been figured, as for example, *Amphibian Coprolites*, *Fish Spine*, etc.; likewise in the same class comes all figured material to which no specific name has been assigned, as *Cythere?* sp., *Palaeoniscus* sp., etc. Such entries are marked *figured*.

In conclusion, the catalogue contains 277 entries, of which there are 57 holotypes, 16 paratypes, 36 cotypes, 124 plesiotypes, 27 chiotypes, 3 plastotypes, and 14 figured specimens. The following tables show the number of types and figured specimens from the several systems, and the zoological distribution of these in the different phyla and classes of the animal kingdom.

TABLE I.
SHOWING THE NUMBER OF TYPES IN THE SEVERAL SYSTEMS.

Group	System	Number of Types
Paleozoic	Ordovician	27
	Silurian	55
	Devonian	27
	Mississippian	15
	Pennsylvanian	135
	Permian	17
Cenozoic	Pleistocene	1

Marking of Types.

For the marking of type fossils in the Geological Museum at The Ohio State University small colored stars are used—red for primary types as well as for plastotypes, and green for secondary or supplementary types. A star is affixed both to the specimen and to its label, and thus the types can be easily singled out in an exhibition case of fossils

TABLE II.
SHOWING ZOOLOGICAL DISTRIBUTION OF TYPES.

Phylum	Number of Types	Class	Number of Types
Protozoa	3	Sarcodina Order Foraminifera	3
Porifera	2	Silicispongiæ	1
		Calcispongiæ	1
Coelenterata	10	Anthozoa	9
		Hydrozoa	1
Vermes	1	Chætopoda	1
Echinodermata	13	Cystoidea	1
		Blastoidea	1
		Crinoidea	10
		Echinoidea	1
Molluscoidea	88	Bryozoa	11
		Brachiopoda	77
Mollusca	145	Pelecypoda	76
		Gastropoda	41
		Scaphopoda	2
		Cephalopoda	26
Arthropoda	6	Crustacea	5
		Arachnida Order Eurypterida	1
Vertebrata	19	Pisces	16
		Amphibia	2
		Mammalia	1

ALPHABETICAL CATALOGUE

- 14034 *Acanthopecten carboniferous* Stevens. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 308, Pl. XV,
Fig. 4.
- 14035 *Acanthopecten ohioensis* Mark. Holotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 308, Pl. XV,
Fig. 5.
- 3743 *Acervularia davidsoni* Edwards and Haime.
See *Stylastrea anna*.
- 14050 *Aclisina? cancellatus* Mark. Holotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 315, Pl. XVI,
Fig. 11.
- 14048 *Aclisina conditi* Mark. Cotypes (2).
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 314, Pl. XVI,
Figs. 8, 9.
- 14051 *Aclisina (?) costata* Mark. Holotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 315, Pl. XVI,
Fig. 12.
- 14047 *Aclisina formosa* Mark. Holotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 314, Pl. XVI,
Fig. 7.
- 14052 *Aclisina (?) ornata* Mark. Holotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 316, Pl. XVI,
Fig. 13.
- 14049 *Aclisina pumila* Mark. Holotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 314, Pl. XVI,
Fig. 10.
- 14045 *Aclisina stevensana* (Meek and Worthen). Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 313, Pl. XVI,
Fig. 5.
- 14046 *Aclisina swallovana* (Geinitz). Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 313, Pl. XVI,
Fig. 6.
= *Pleurophorella geintzi*.

- 14038 *Allerisma geinitzi* Meek. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 310, Pl. XV,
Fig. 11.
- 4668 *Allerisma terminale* Hall. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 234, Pl.
XIII, Fig. 15.
- 14024 *Ambocoelia planoconvexa* (Shumard). Plesiotype.
Ames limestone, Conemaugh (Penn.). Athens, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 304, Pl. XIV,
Figs. 5, 6.
- 13309 *Ambocoelia umbonata* var. *gregaria* Hall. Plesiotypes (2).
Chagrin (Up. Dev.). Road two miles east of Trumbull
Center, Trumbull Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 539, Pl. XXXI,
Figs. 6-9.
- 9062 *Amphicoelia* (*Leptodomus*?) *costata* Hall and Whitfield. Holotype.
Niagaran (Sil.). Cedarville, Greene Co., Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 140, Pl. VII, Fig. 23.
MILLER. *N. Am. Geol. and Pal.*, 1889, p. 461, Fig. 773.
- 15256 *Anthraconeilo bownockeri* Morningstar. Holotype.
Sharon ore, Pottsville (Penn.). Near mouth of Lick Run,
Scioto Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 208,
Pl. X, Fig. 21.
- 15161 *Anthracopupa* (?) *dunkardana* Stauffer and Schroyer. Cotypes (5).
to Lower Washington limestone, Dunkard (Perm.). One-half
15164 mile south of Pleasant Grove, Belmont Co., Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 144, Pl. XI, Figs. 12-16.
- 15211 *Archaeocidaris spine*. Figured.
Lower Mercer limestone, Pottsville (Penn.). Vernon Tp.,
Scioto Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 156,
Pl. VI, Fig. 15.
- 15291 *Astartella concentrica* (Conrad). Plesiotypes (2).
15292 Upper Pottsville (Penn.). Carbon Hill, Hocking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 241, Pl.
XIII, Figs. 12, 13.
- 15293 *Astartella newberryi* Meek. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Southeast of
Frazeyburg, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 242,
Pl. XIII, Fig. 14.

- 14042 *Astartella portersvillensis* Mark. Cotypes (2).
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 311, Pl. XV,
Figs. 15, 16.
- 15298 *Astartella varica* McChesney. Plesiotypes (2).
- 15299 Upper Pottsville (Penn.). Carbon Hill, Hocking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 243,
Pl. XIV, Figs. 1, 2.
- 15300 *Astartella varica* McChesney. Plesiotype.
McArthur limestone, Pottsville (Penn.). Elk Tp., Vinton
Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 243,
Pl. XIV, Fig. 3.
- 14040 *Astartella vera* Hall. Plesiotype.
Brush Creek limestone, Conemaugh (Penn.). Trimble, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 311, Pl. XV,
Fig. 13.
- 14041 *Astartella vera* Hall. Plesiotype.
Ames limestone, Conemaugh (Penn.). Caldwell, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 311, Pl. XV,
Fig. 14.
- 9012 *Athyris* (*Seminula*?) sp. Figured.
Waverly (Miss.). Sciotoville, Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 2, 1894, p. 83, Pl.
XLVII, Fig. 35.
- 13310 *Athyris polita* Hall. Plesiotypes (2).
- 13311 Chagrin (Up. Dev.). Chippewa Creek, Cuyahoga Co., and
Trumbull Creek, one-fourth mile south of Trumbull Center,
Trumbull Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 540, Pl. XXXI,
Figs. 10, 11.
- 15225 *Aulacorhynchus millepunctatus* Meek and Worthen. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Vernon Tp.,
Scioto Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 180, Pl.
VII, Fig. 12.
- 3208 *Avicula whitfieldi* Foerste. Holotype.
Brassfield (Sil.). Todd's Fork, Wilmington, Ohio.
FOERSTE. *Geol. Surv. Ohio*, Vol. VII, 1893, p. 558, Pl. 37, Fig. 5.
See *Cypricardites ferrugineum*.
= *Cyrtodonta* (?) *ferruginea*.
- 14033 *Aviculopecten herzeri* Meek. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 307, Pl. XIII,
Fig. 3.
MORNINGSTAR. *Idem*. Bull. 25, 1922, p. 226, Pl. XIII, Fig. 3.

- 15246 *Aviculopecten herzeri* Meek. Plesiotype.
McArthur limestone, Pottsville (Penn.). Elk Tp., Vinton Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 226, Pl. XIII, Fig. 4.
- 15213 *Bascomella gigantea* Morningstar. Cotypes (13).
McArthur limestone, Pottsville (Penn.). Monroe Furnace, Jackson Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 157, Pl. VI, Figs. 18-20.
- 2827 *Batostoma jamesi* (Nicholson). Paratypes (9).
See *Chaeteles jamesi*.
Berenicea elkhornensis Shideler mss. Chirotype.
Elkhorn, Cincinnati (Ord.). Richmond, Indiana.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.
Brachiospongia maysvillensis Shideler mss. Chirotype.
Mt. Hope, Cincinnati (Ord.). Ripley, Ohio.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.
- 12208 *Bulimorpha canaliculata* Hall. Plesiotype.
Maxville (Miss.). Cut 4, Mt. Perry, Fultonham, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911, p. 400, Fig. 25.
- 14054 *Bulimorpha minuta* (Stevens). Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 317, Pl. XVI, Fig. 15.
- 13256 *Camarotoechia contracta* Hall. Plesiotypes (7).
- 13262 Chagrin (Up. Dev.). Mill Creek, two miles north of Jefferson,
to Ashtabula Co., Ohio.
- 13267 PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 544, Pl. XXXII, Figs. 14-20.
- 3515 *Camarotoechia hydraulica* (Whitfield). Holotype.
Greenfield dolomite, Monroe (Sil.). Greenfield, Ohio.
GRABAU. *Geol. Surv. Mich.*, Ser. 1, 1909, p. 128, Pl. 30, Fig. 17.
See *Rhynchonella hydraulica*.
- 13268 *Camarotoechia orbicularis* Hall and Clarke. Plesiotypes (2).
- 13269 Chagrin (Up. Dev.). Madison-Thompson road, three miles south of Madison, Lake Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 532, Pl. XXVIII, Figs. 7, 8.
- 10422 *Ceramopora* (?) *beani* James. Holotype.
Cincinnati (Ord.). Lebanon, Ohio.
JAMES. *Paleontologist* No. 1, 1878, p. 5; Jour. Cinci. Soc. Nat. Hist., Vol. 7, 1884, p. 23, Figs. 3, 3b.
= *Paleschaera beani*.

- 2827 *Chaetetes jamesi* Nicholson. Paratypes (9).
Eden shale, Cincinnati (Ord.). Cincinnati, Ohio.
NICHOLSON. *Quart. Jour. Geol. Soc. London*, 30, 1874, p. 506, Pl. 29,
Figs. 10, 10b; Pal. Ohio, Vol. II, 1875, p. 200, Pl. 21, Figs. 11, 11b.
= *Batostoma jamesi*.
- Chasmops pulchra* Shideler mss. Chirotype.
Liberty, Cincinnati (Ord.). Oxford, Ohio.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.
- 15228 *Chonetes choteauensis* Mather. Plesiotypes (3).
- 15229 Lowellville limestone, Pottsville (Penn.). Poverty Run,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 178, Pl.
VII, Figs. 16-18.
- 14015 *Chonetes granulifera* Owen. Plesiotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 200, Pl. XIII,
Fig. 3.
- 15226 *Chonetes mesolobus* Norwood and Pratten. Plesiotypes (2).
- 15227 Lower Mercer limestone, Pottsville (Penn.). Southeast of
Frazeyburg, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 179,
Pl. VII, Figs. 14, 15.
- 13270 *Chonetes minutus* Prosser. Cotypes (4).
to Chagrin (Up. Dev.). Run, two miles south of Monroe Center,
13272 Ashtabula Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 540, Pl.
XXXII, Figs. 1-5.
- 13273 *Chonetes scitulus* Hall. Plesiotype.
Chagrin (Up. Dev.). Tinkers Creek, Cuyahoga Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 541, Pl.
XXXII, Fig. 6.
- 14016 *Chonetes verneuillanus* Norwood and Pratten. Plesiotypes (2).
Portersville limestone, Conemaugh (Penn.). Blue Rock Tp.,
Muskingum Co., Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 301, Pl. XIII,
Figs. 4, 5.
- 12197 *Cleiothyris hirsuta* Hall. Plesiotype.
Maxville (Miss.). Harper Shaft, Olive Furnace, Ohio.
MORSE, *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911,
p. 388, Fig. 15.
- 3208 *Clidophorus ferrugineus* (Foerste). Holotype.
See *Nuculites (Cleidophorus) ferrugineum*.
- 8909 *Colummaria alveolata* Goldfuss.
See *Favistella stellata*. Plesiotype?
- 14026 *Composita subtilita* (Hall). Plesiotype (4).
Cambridge limestone, Conemaugh (Penn.). Langsville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 305, Pl. XIV,
Figs. 9, 10.

- 15235 *Composita subtilita* (Hall). Plesiotypes (4).
to Lower Mercer limestone, Pottsville (Penn.). Southeast of
15238 Frazeyburg, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 192, Pl. VIII, Figs. 10-13.
- 7293B *Conchidium colletti* (Miller). Plesiotype.
Niagaran (Sil.). Three miles above Logansport, Indiana.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 2, 1895, p. 235, Pl. LXVI, Figs. 16, 17.
- 7296 *Conchidium obsoletum* Hall and Clarke. Holotype and Paratypes (5).
Guelph (Sil.). Genoa, Ottawa Co., Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 2, 1895, Pl. LXVII, Figs. 8, 9; 14th Rep. State Geol. New York for 1894, 1897, p. 366, Pl. 11, Figs. 1, 2; 48th Rep. New York State Mus. for 1895, 2, 1897, p. 366, Pl. 11, Figs. 1, 2.
- 15188 *Coprolites*, probably from Amphibians. Figured (4).
to Creston Reds, Dunkard (Perm.). One mile east of Elba, Ohio.
- 15191 STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920, p. 147, Pl. XIII, Figs. 41-44.
- 15177 *Coprolites*, probably from Fishes. Figured (6).
to Elm Grove limestone, Dunkard (Perm.). Raven Rocks, two
15182 miles north of Beallsville, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920, p. 146, Pl. XII, Figs. 30-35.
- 14083 *Corallidomus concentrica* Whitfield. Cotype.
Liberty, Richmond (Ord.). Brown Co., Ohio.
WHITFIELD. *Geol. Surv. Ohio*, Vol. VII, 1893, p. 492, 493, Fig. 2; Pl. XIII, Fig. —.
ULRICH. *Idem.*, p. 493, Pl. LV, Figs. 15, 16.
- Cornulites striatus* Shideler mss. Chirotype.
McMicken, Cincinnati (Ord.). Cincinnati, Ohio.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.
- 15288 *Crenipecten foerstii* Herrick. Plesiotypes (2).
15289 Lower Mercer limestone, Pottsville (Penn.). Southeast of
Frazeyburg, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 230, Pl. XIII, Figs. 7, 8.
- 15206 *Crinoid Stems*. Figured (5).
to Lower Mercer limestone, Pottsville (Penn.). Symmes Creek,
15210 Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 155, Pl. VI, Figs. 9-13.
- 2999 *Cuneamya miamiensis* Hall and Whitfield. Paratypes (9).
Waynesville, Richmond (Ord.). Waynesville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 9, Pl. II, Figs. 9, 10.
- 2995 *Cuneamya scapha* Hall and Whitfield. Holotype.
Waynesville, Richmond (Ord.). Near Waynesville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 92, Pl. II, Fig. 2.

- 12202 *Cypricardella oblonga* Hall. Plesiotype.
Maxville (Miss.). Cut 4, Mt. Perry-Fultonham, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911,
p. 394, Fig. 20.
- 4610 *Cypricardinia* (?) *carbonaria* Meek. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Bald Knob,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 244,
Pl. XI, Fig. 14.
- 3208 *Cypricardites ferrugineum* Hall and Whitfield. Holotype.
Brassfield (Sil.). Todd's Fork, Wilmington, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 116, Pl. V, Fig. 11.
See *Avicula whitfieldi*.
= *Cyrtodonta* (?) *ferruginea*.
- 13275 *Cyrtia alta* Hall. Plesiotype.
Chagrin (Up. Dev.). Three miles south of Madison, Geauga
Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 536, Pl. XXX,
Fig. 4.
- 5887 *Cyrtoceras herzeri* Hall and Whitfield. Holotype.
Niagaran (Sil.). Cedarville, Greene Co., Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 150, Pl. VIII, Figs. 8, 9.
= *Hexamoceras herzeri*.
- 3431 *Cyrtoceras myrice* Hall and Whitfield. Paratypes (2).
14803 Niagaran (Sil.). Yellow Springs, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 149, Pl. VIII, Fig. 9.
= *Kionoceras myrice*.
- 14802 *Cyrtoceras cf. myrice* Hall and Whitfield. Paratype.
Niagaran (Sil.). Yellow Springs, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 149, Pl. VIII, Fig. 9.
= *Kionoceras myrice*.
- 3411 *Cyrtoceras percurvatum* Foerste mss. Chiroholotype.
Niagaran (Sil.). Yellow Springs, Ohio.
FOERSTE, *Manuscript on Silurian Cephalopoda*.
- 14805 *Cyrtoceras radiceforme* Foerste mss. Chiroholotype.
Niagaran (Sil.). Yellow Springs, Ohio.
FOERSTE, *Manuscript on Silurian Cephalopoda*.
- 3208 *Cyrtodonta* (?) *ferruginea* (Hall and Whitfield). Holotype.
See *Avicula whitfieldi* and *Cypricardites ferrugineum*.
- 15171 *Cythere* (?) sp. Figured (6).
to Elm Grove limestone, Dunkard (Perm.). Little Short Creek,
15176 Martins Ferry, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 146, Pl. XI, Figs. 24-29.

- 13276 *Dalmanella tioga* var. *elmira* Williams. Plesiotypes (3).
to Chagrin (Up. Dev.). Chippewa Creek, Cuyahoga Co.,
13278 Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 530, Pl. XXVIII, Figs. 1-6.
- 3428 *Dawsonoceras annulatum* (Sowerby). Paratypes (9).
3432 See *Orthoceras annulatum*.
9499
- 15286 *Deltopecten scalaris* (Herrick). Plesiotypes (2).
15287 Lower Mercer limestone, Pottsville (Penn.). Vernon Tp., Scioto Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 228, Pl. XIII, Figs. 5, 6.
- 12203 *Dentalium illinoiense* Worthen. Plesiotype.
Maxville (Miss.). Cut 4, Mt. Perry-Fultonham, Ohio.
MORSE, *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, p. 395, Fig. 21.
= *Laevidentalium illinoiense*.
- 14014 *Derbya crassa* (Meek and Hayden). Plesiotype.
Ames limestone, Conemaugh (Penn.). Deersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 300, Pl. XIII, Fig. 2.
- 15222 *Derbya crassa* (Meek and Hayden). Plesiotype.
Lowellville limestone, Pottsville (Penn.). Poverty Run, Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 176, Pl. VII, Fig. 9.
- 15223 *Derbya crassa* (Meek and Hayden). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Bald Knob, Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 176, Pl. VII, Fig. 10.
- 15224 *Derbya robusta* (Hall). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Vernon Tp., Scioto Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 177, Pl. VII, Fig. 11.
- 10419 *Dermatostroma scabrum* (James). Holotype.
See *Stromatopora scabra*.
- 7304 *Discoceras graftonense* (Meek and Worthen). Chiroplesiotype.
Niagaran (Sil.). Rising Sun, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 7057 *Discoceras ortonii* (Meek). Chiroplesiotype.
Niagaran (Sil.). Wilmington, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.

- 3404 *Discoceras ortonii* (Meek). Holotype.
Niagaran (Sil.). Greenville, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
See *Lituities* (?) *ortonii* Meek.
- 9003 *Dicraniscus ortonii* Meek. Cotype.
Top of Brassfield (Sil.). Near Dayton, Ohio.
MEEK. *Am. Jour. Sci.*, Third Ser., Vol. 4, 1872, p. 283.
= *Triplecia ortonii*.
- 8569 *Dictyostroma undulatum* Nicholson. Holotype.
Niagaran (Sil.). Louisville, Kentucky.
NICHOLSON. *Pal. Ohio*, Vol. II, 1875, p. 254, Pl. 24, Figs. 6-6c.
- 15187 *Diplodus washingtonensis* Stauffer and Schroyer. Holotype.
Lower Washington limestone, Dunkard (Perm.). North end
of Shadyside, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 147, Pl. XIII, Fig. 40.
- 15192 *Edaphosaurus* sp. (Neural spine). Figured (2).
- 15193 Creston Reds, Dunkard (Perm.). Marietta, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 147, Pl. XIII, Figs. 45, 46.
- 14027 *Edmondia aspinwallensis* Meek. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1920, p. 305, Pl. XIV,
Fig. 11.
MORNINGSTAR. *Idem.*, Bull. 25, 1922, p. 197, Pl. X, Fig. 7.
- 15257 *Edmondia gibbosa* (McCoy). Plesiotypes (2).
- 15258 Lower Mercer limestone, Pottsville (Penn.). Southeast of
Fairview School, Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 197,
Pl. X, Figs. 4, 5.
- 15259 *Edmondia meekiana* (Herrick)? Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 198,
Pl. X, Fig. 6.
- 15158 *Edmondia* (?) *minuta* Stauffer and Schroyer. Holotype.
Washington limestone, Dunkard (Perm.). Shadyside, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 144, Pl. XI, Fig. 9.
- 15260 *Edmondia ovata* Meek and Worthen. Plesiotypes (2).
- 15261 Lower Mercer limestone, Pottsville (Penn.). Bald Knob,
Licking Co., and southeast of Fairview School, Muskingum
Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 199, Pl. X,
Figs. 8, 9.

- 14028 *Edmondia reflexa* Meek. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 305, Pl. XIV,
Fig. 12.
- 15159 *Edmondia* (?) *washingtonensis* Stauffer and Schroyer. Cotype.
Cassville shale Dunkard (Perm.). Beckett Station, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 144, Pl. XI, Fig. 10.
- 15160 *Edmondia* (?) *washingtonensis* Stauffer and Schroyer. Cotype.
Lower Washington limestone, Dunkard (Perm.). Shadyside,
Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 144, Pl. XI, Fig. 11.
- 15290 *Entolium aviculatum* Swallow. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Rock Cut,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 232,
Pl. XIII, Fig. 9.
- 14036 *Entolium prosseri* Mark. Cotypes (3).
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 309, Pl. XV,
Figs. 6-8.
- 13867 *Eucalyptocrinus proboscidalis* Miller. Holotype and Plastotype.
8263 Cedarville dolomite (Sil.). Pontiac, five miles northeast of
Piqua, Ohio.
MILLER. *Jour. Cinci. Soc. Nat. Hist.*, Vol. V, 1882, p. 224, Pl. IX, Fig. 2.
FOERSTE. *Ohio Jour. Sci.*, Vol. XXI, No. 2, Dec., 1920, p. 70, Fig. 4.
- 3299 *Eucalyptocrinus splendidus* Hall and Whitfield. Holotype.
Niagaran (Sil.). Springfield, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 128, Pl. VI, Fig. 12.
- 12196 *Eumetria marcyi* Shumard. Plesiotype.
Maxville (Miss.). Olive Furnace, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911, p.
386, Fig. 14.
- 9787 *Eupachyrcrinus mooresi* (Whitfield). Plesiotypes (2).
15205 Upper Pottsville (Penn.). Carbon Hill, Hocking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 154,
Pl. VI, Figs. 7, 8.
- 15308 *Euphemus carbonarius* (Cox). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 249,
Pl. XV, Figs. 4, 5.
- 15306 *Euphemus nodocarinatus* (Hall). Plesiotypes (2).
15307 Upper Pottsville (Penn.). Carbon Hill, Hocking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 249,
Pl. XV, Figs. 1, 2.

- 4478 *Eurylepis corrugatus* Newberry. Holotype.
Upper Freeport, Allegheny (Penn.). Linton, Ohio.
NEWBERRY. *Proc. Acad. Nat. Sci. Phil.*, loc. cit.; *Pal. Ohio*, Vol. I, 1873,
p. 350, Pl. 38, Figs. 4, 4a.
- 4514 *Eurylepis insculptus* Newberry. Holotype.
Upper Freeport, Allegheny (Penn.). Linton, Ohio.
NEWBERRY. *Proc. Acad. Nat. Sci. Phil.*, loc. cit.; *Pal. Ohio*, Vol. I,
1873, p. 351, Pl. XXXIX, Figs. 2, 2a.
- 4565 *Eurylepis lineatus* Newberry. Holotype.
Upper Freeport, Allegheny (Penn.). Linton, Ohio.
NEWBERRY. *Proc. Acad. Nat. Sci. Phil.*, loc. cit.; *Pal. Ohio*, Vol. I, 1873,
p. 353, Pl. 39, Figs. 7, 7a.
- 4563 *Eurylepis ovoideus* Newberry. Holotype.
Upper Freeport, Allegheny (Penn.). Linton, Ohio.
NEWBERRY. *Proc. Acad. Nat. Sci. Phil.*, loc. cit.; *Pal. Ohio*, Vol. I,
1873, p. 351, Pl. XXXIX, Fig. 1.
- 4508 *Eurylepus striolatus* Newberry. Holotype.
Upper Freeport, Allegheny (Penn.). Linton, Ohio.
NEWBERRY. *Pal. Ohio*, Vol. I, 1873, p. 355.
- 3510 *Eurypteris eriensis* Whitfield. Cotype.
Put-in-Bay dolomite, Monroe (Sil.?). Lake Erie, Ohio.
WHITFIELD. *Ann. New York Acad. Sci.* Vol. II, 1882, p. 196; *Idem.*, Vol.
V, 1891, p. 515, Pl. V, Fig. 32; *Geol. Surv. Ohio*, Vol. VII, 1893; p.
416, Pl. I, Fig. 32.
GRABAU. *Geol. Surv. Mich.*, Ser. 1, 1919, p. 208, Pl. XXX, Fig. 32.
= *Eurypteris microphthalmus*.
- 3510 *Eurypteris microphthalmus* Hall.
See *Eurypteris eriensis*. Cotype.
- 3756 *Favosites pleurodictyoides* Nicholson. Cotype.
Columbus limestone (Dev.). Kelley's Island, Ohio.
NICHOLSON. *Pal. Ohio*, Vol. II, 1875, p. 231, Pl. XXIII, Figs. 3, 3b.
- 8909 *Favistella stellata* Hall. Plesiotype?
Richmond (Ord.). Cincinnati, Ohio.
NICHOLSON. *Pal. Ohio*, Vol. II, 1875, p. 185.
= *Columnaria alveolata*.
- 3292 *Fenestella nervata* Nicholson. Holotype.
Niagaran (Sil.). Cedarville, Ohio.
NICHOLSON. *Pal. Ohio*, Vol. II, 1875, p. 264, Pl. XXV, Figs. 11, 11a.
= *Ptiloporella nervata*.
- 15184 *Fish plate* (probably cranial plate). Figured.
Elm Grove limestone, Dunkard (Perm.). Raven Rocks,
Belmont Co., Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 146, Pl. XIII, Fig. 37.

- 15183 *Fish spine (Elasmobranch)*. Figured.
Shales above Waynesburg "A" Coal, Dunkark (Perm.).
Clarinton, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 146, Pl. XII, Fig. 36.
- 15202 *Fusulina secatica* (Say). Plesiotype.
Upper Mercer flint, Pottsville (Penn.). Near Rock Cut,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 153, Pl.
VI, Fig. 3.
- 15203 *Girtyina ventricosa* (Meek and Worthen). Plesiotype.
Upper Mercer flint, Pottsville (Penn.). East of Mohawk
Village, Coshocton Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, P. 153, Pl.
VI, Fig. 4.
- 7670 *Glossina flabellula* Hall and Clarke. Cotype.
Berea sandstone, Waverly (Miss.). Berea, Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 1, 1892, p. 172, Pl. I,
Fig. 34.
HALL. *14th Ann. Rep. New York State Geol.*, 1894, p. 326, Pl. I, Fig. 6.
- 15218 *Glossina waverlyensis* (Herrick). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Southeast of
Frazeyburg, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 169, Pl.
VII, Fig. 4.
- 15157 *Glossites (?) belmontensis* Stauffer and Schroyer. Holotype.
Elm Grove limestone, Dunkard (Perm.). Little Short Creek,
west of Martins Ferry, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 144, Pl. XI, Fig. 8.
- 3082 *Gomphoceras eos* Hall and Whitfield. Holotype.
Richmond (Ord.). Near Dayton, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 100, Pl. 3, Fig. 5.
- 8736 A, B, *Gomphocystites bownockeri* Foerste. Holotype and Paratype.
Niagaran (Sil.). Cedarville, Ohio.
FOERSTE. *Ohio Jour. Sci.*, Vol. XXI, No. 2, Dec., 1920, p. 57, Pl. III,
Figs. 1a, b.
- Hallopora crassa* Shideler mss. Chirotype.
Arnheim, Cincinnati (Ord.). Russellville, Ohio.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.
- Hemicystites edenensis* Shideler mss. Chirotype.
McMicken, Cincinnati (Ord.). Cincinnati, Ohio.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.
- Hemiphragma subglobosa* Shideler mss. Chirotype.
Economy, Cincinnati (Ord.). Ripley, Ohio.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.

- 15314 *Hemizyga* sp. Figured.
Lower Mercer limestone, Pottsville (Penn.). Bald Knob,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*. Fourth Ser., Bull. 25, 1922, p. 260,
Pl. XV, Fig. 25.
- 10424 *Heterocrinus juvenis* Hall. Plesiotype.
Maysville (Corryville) limestone, Cincinnati (Ord.). Lebanon,
Ohio.
MEEK. *Pal. Ohio*, Vol. I, 1873, p. 10, Pl. 1, Figs. 3a, b.
- 5887 *Hexamoceras herzeri* (Hall and Whitfield). Holotype.
Niagaran (Sil.). Cedarville, Greene Co., Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
See *Cyrtoceras herzeri*.
- 3528 *Hindella* (?) (*Greenfieldia*) *whitfieldi* Grabau.¹ Cotype.
Greenfield dolomite, Monroe (Sil.?). Greenfield, Ohio.
GRABAU. *Geol. Surv. Mich.*, Ser. 1, 1909, p. 149, Pl. XXX, Fig. 8.
See *Meristella bella*.
- Homotrypella elegans* Shideler mss. Chirotype.
Whitewater, Cincinnati (Ord.). Oxford, Ohio.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.
- Homotrypella ramosa* Shideler mss. Chirotype.
Arnheim, Cincinnati (Ord.). Russellville, Ohio.
SHIDELER. *Manuscript on Cincinnati Fossils from Southwestern Ohio*.
- 14025 *Hustedia mormoni* (Marcou). Plesiotype.
Ames limestone, Conemaugh (Penn.). Steubenville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 304, Pl. XIV,
Figs. 7, 8.
MORNINGSTAR. *Idem.*, Bull. 25, 1922, p. 192, Pl. IX, Figs. 28, 29.
- 3329 *Illaenus (Bumastus) insignis* (?) Meek (not Hall). Holotype.
Niagaran (Sil.). Springfield, Ohio.
MEEK. *Pal. Ohio*, Vol. I, 1873, p. 189, Pl. XV, Figs. 5a, b, c.
= *Illaenus springfieldensis*.
- 3329 *Illaenus (Bumastus) springfieldensis* Meek. Holotype.
Niagaran (Sil.). Springfield, Ohio.
MEEK, *Pal. Ohio*, Vol. I, 1873, p. 192.
See *Illaenus (Bumastus) insignis*?
- 3238 *Inocaulis bella* Hall and Whitfield. Holotype.
Niagaran (Sil.). Yellow Springs, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 122, Pl. VI, Fig. 2.
= *Palaeodictyota bella*.

¹ A detailed study of this specimen by Dr. J. Ernest Carman has shown that it belongs to neither of the genera *Hindella* nor *Meristella*. The umbonal region was etched with HCl with the result that the pedical valve was seen to be provided with two septae which converge slightly forward and which extend anteriorly one-third the length of the valve—features which are characteristic of the genus *Prosserella*, but not of *Hindella* or *Meristella*. This form is then a *Prosserella*, and probably the locality reference is in error.

- 3431 *Kionoceras myrice* (Hall and Whitfield). Paratype.
See *Cyrtoceras myrice*.
- 14803 *Kionoceras myrice* (Hall and Whitfield). Paratype.
Niagaran (Sil.). Yellow Springs, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
See *Cyrtoceras myrice*.
- 14802 *Kionoceras* cf. *myrice* (Hall and Whitfield). Paratype.
Niagaran (Sil.). Yellow Springs, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
See *Cyrtoceras myrice*.
- 12203 *Laevidentalium illionoisense* (Worthen). Plesiotype.
See *Dentalium illinoisense*.
- 14031 *Leda meekana* Mark. Holotype.
Portersville limestone, Conemaugh (Penn.). Portersville,
Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 307, Pl. XV,
Fig. 1.
MORNINGSTAR. *Idem.*, Bull. 25, 1922, p. 206, Pl. X, Figs. 25, 26.
- 15254 *Leda prolongata* Morningstar. Holotype.
Lower Mercer limestone, Pottsville (Penn.). Fairview School,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 206,
Pl. X, Fig. 28.
- 14037 *Lima retifera* Shumard. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 309, Pl. XV, Fig. 9.
MORNINGSTAR. *Idem.*, Bull. 25, 1922, p. 233, Pl. XIII, Fig. 10.
- 15215 *Lingula carbonaria* Shumard. Plesiotype.
Anthony coal, Pottsville (Penn.). Scioto Furnace, Scioto Co.,
Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 166, Pl.
VII, Fig. 1.
- 15216 *Lingula carbonaria* Shumard. Plesiotypes (2).
- 15217 Upper Mercer limestone, Pottsville (Penn.). Elk Tp., Vinton
Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 166, Pl.
VII, Figs. 2, 3.
- 15151 *Lingula permiana* Stauffer and Schroyer. Cotypes (4).
to Washington limestone, Dunkard (Perm.). Near Crabapple,
15154 Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 143, P. XI, Figs. 1-5.
- 13259 *Liorhynchus ashtabulense* Prosser. Cotypes (4).
- 13279 Chagrin (Up. Dev.). Run two miles south of Monroe Center,
to Ashtabula Co., Ohio.
- 13281 PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 546, Pl.
XXXIII, Figs. 5-8.

- 13260 *Liorhynchus clarkei* Prosser. Cotypes (7).
13261 Chagrin (Up. Dev.). Mill Creek, two miles north of Jefferson,
13282 Ashtabula Co., Ohio.
to PROSSER. *Geol. Surv. Ohio*. Fourth Ser., Bull. 15, 1912, P. 545, Pl.
13285 XXXII, Figs. 21-23; Pl. XXXIII, Figs. 1-4.
- 13286 *Liorhynchus globuliforme* var. *chagrinanum* Prosser. Cotypes (3).
to Chagrin (Up. Dev.). Three miles south of Madison, Lake
13288 Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 533, Pl. XXIX,
Figs. 1, 2; Pl. XXVIII, Figs. 14, 15.
- 13258 *Liorhynchus newberryi* Hall. Plesiotype.
Chagrin (Up. Dev.). Run two miles south of Monroe Center,
Ashtabula Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 546, Pl.
XXXIII, Fig. 10.
- 13294 *Liorhynchus newberryi* Hall. Plesiotype.
Chagrin (Up. Dev.). Mill Creek, Eagleville, Ashtabula Co.,
Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 546, Pl.
XXXIII, Fig. 9.
- 13289 *Liorhynchus ohioense* Prosser. Cotypes (5).
to Chagrin (Up. Dev.). Trumbull Creek, Trumbull Co., and
13293 north of Gates Mill, Cuyahoga Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 532, Pl.
XXVIII, Figs. 9-13.
- 3404 *Lituites* (?) *ortoni* Meek. Holotype.
Niagaran (Sil.). Greenville, Ohio.
MEEK. *Pal. Ohio*, Vol. I, 1873, p. 186, Pl. 15, Fig. 4.
(*Gyroceras ortoni* at end of description).
= *Discoceras ortoni*.
- 14013 *Lophophyllum profundum* (Milne-Edwards and Haime). Plesio-
type.
Ames limestone, Conemaugh (Penn.). Deersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 300, Pl. XIII,
Fig. 1.
- 15204 *Lophophyllum profundum* (Milne-Edwards and Haime). Plesio-
type.
Lower Mercer limestone, Pottsville (Penn.). Near White
Cottage, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 154, Pl.
VI, Fig. 5.
- 15165 *Loxonema* (?) *parva* Stauffer and Schroyer. Cotypes (4).
to Lower Washington limestone, Dunkard (Perm.). One-half
15168 mile south of Pleasant Grove, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 145, Pl. XI, Figs. 17-21.
- 14044 *Loxonema scitulum* Meek and Worthen. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 312, Pl. XVI,
Fig. 2.

- 9792 *Marginifera muricata* var. *missouriensis* Girty. Plesiotypes (3).
Upper Pottsville (Penn.). Carbon Hill, Hocking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 184, Pl. IX, Figs. 1-3.
- 15327 *Marginifera muricata* var. *missouriensis* Girty. Plesiotypes (2).
Lower Mercer limestone, Pottsville (Penn.). Near White Cottage, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 184, Pl. IX, Figs. 4, 5.
- 14019 *Marginifera wabashensis* (Norwood and Pratten). Plesiotype.
Cambridge limestone, Conemaugh (Penn.). Norwich, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 185, Pl. IX, Fig. 10.
See *Productus longispinus*.
- 15318 *Marginifera wabashensis* (Norwood and Pratten). Plesiotypes (3).
to Lower Mercer limestone, Pottsville (Penn.). Near white
15320 Cottage, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 185, Pl. IX, Figs. 6-9.
- 3316 *Marsipocrinus praematurus* (Hall and Whitfield). Paratypes (18).
3323 See *Platycrinus praematurus*.
- 15758 *Megalonyx jeffersoni* Desmarest. Plesiotype.
Pleistocene. Berlin Tp., Holmes Co., Ohio.
CLAYPOLE. *Am. Geol.*, Vol. VII, 1891, pp. 122-132, 149-153.
OSBORN. *Age of Mammals*, 1910, p. 465, Fig. 203.
HAY. *Geol. Surv. Ind.*, Vol. XXXVI, 1911, p. 558; *Geol. Surv. Iowa*, Vol. XXIII, 1912, p. 107.
- 3962 *Melanocrinus bainbridgensis* Hall and Whitfield. Cotypes (4).
to Huron shale (Up. Dev.). Bainbridge, Ohio.
- 3965 HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 158, Pl. 13, Figs. 2-3.
- 3528 *Meristella bella* Whitfield (not Hall.)¹ Cotype.
Greenfield dolomite, Monroe (Sil.). Greenfield, Ohio.
WHITFIELD. *Ann. New York Acad. Sci.*, Vol. 5, 1891, p. 510, Pl. 5, Fig. 8;
Geol. Surv. Ohio, Vol. VII, 1893, p. 412, Pl. I, Fig. 8.
SHERZER. *Geol. Surv. Mich.*, Vol. VII, Pl. I, 1900, p. 223, Pl. XVII, Fig. 8.
= *Hindella* (?) (*Greenfieldia*) *whitfieldi*.
- 8995 *Metacoceras pottsvillensis* Morningstar. Holotype.
Lower Mercer limestone, Pottsville (Penn.). Near Hanging Rock, Lawrence Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 269, Pl. XVI, Figs. 7, 8.
- 3023 *Modiolodon oviformis* (Ulrich). Paratypes? (2).
Trenton (Ord.). Frankfort, Kentucky.
ULRICH. *Geol. Surv. Ohio*, Vol. VII, 1893, p. 652, Pl. LIII, Fig. 7.
See *Modiolopsis oviformis*.

¹ See footnote under *Hindella* (?) (*Greenfieldia*) *whitfieldi*, p. 47.

- 3024 *Modiolopsis cincinnatiensis* Hall and Whitfield. Cotype.
Cincinnatian (Ord.). Cincinnati, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 88, Pl. II, Fig. 14.
= *Whiteavesia cincinnatiensis*.
- 3023 *Modiolopsis oviformis* Ulrich. Paratypes? (2).
Trenton (Ord.). Frankfort, Kentucky.
ULRICH. *Am. Geol.*, Vol. V, 1890, p. 276, Figs. 4a-c.
= *Modiolodon oviformis*.
- 7022 A, B *Monomerella greeni* Hall. Holotype and Paratype.
Guelph dolomite, Niagaran (Sil.). Rising Sun, Wood Co., Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 1, 1892, pp. 42, 175,
Pl. 44D, Fig. 6; *14th Rep. State Geol. New York*, for 1894, 1897, p. 328,
Pl. I, Fig. 10; *48th Rep. New York State Mus.*, Vol. II, for 1895,
1897, p. 328, Pl. I, Fig. 10.
- 3145 *Monomerella ortonii* Hall and Clarke. Holotype.
Guelph dolomite, Niagaran (Sil.). Rising Sun, Wood Co., Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 1, 1892, pp. 42, 175,
Pl. 40, Figs. 14, 15; *14th Rep. State Geol. New York* for 1894, 1897,
p. 330, Pl. II, Figs. 4, 5; *48th Rep. New York State Mus.*, Vol. II, for
1895, 1897, p. 330, Pl. II, Figs. 4, 5.
- Monticulipora pernodosa* Shideler mss. Chirotype.
Waynesville, Cincinnatian (Ord.). Oxford, Ohio.
SHIDELER. *Manuscript on Cincinnatian Fossils from Southwestern Ohio*.
- 12214 *Murchisonia vermicula* Hall. Plesiotype.
Maxville (Miss.). Cut 4, Mt. Perry-Fultonham, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911,
p. 409, Figs. 32a, b.
- 15269 *Myalina pernaformis* (Cox). Plesiotypes (3).
to Boggs limestone, Pottsville (Penn.). Near Hopewell P. O.,
15271 Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 217,
Pl. XI, Figs. 7-9.
- 15267 *Myalina pernaformis* (Cox) var. Figured (2).
- 15268 Harrison ore, Pottsville (Penn.). Hamilton Tp., Jackson
Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 218,
Pl. XI, Figs. 5, 6.
- 9819 *Myalina recurvirostris* var. *sinuosa* Morningstar. Cotypes (3).
- 15272 Lower Mercer limestone, Pottsville (Penn.). Near Adams
15273 Mills, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 219,
Pl. XI, Figs. 10-12.
- 4587 *Myalina swallowi* McChesney. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Millersburg, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 219, Pl.
XI, Fig. 13.
- 3953 *Mylostoma terrelli* Newberry. Plastotype.
Cleveland shale (Up. Dev.). Sheffield, Ohio.
NEWBERRY. *Pal. Fishes of N. Am.*, *U. S. Geol. Surv.*, Mono. XVI, 1889,
p. 165, Pl. XIV, Figs. 1, 2.

- 3946 *Mylostoma variabilis* Newberry. Plastotypes (4).
3948 Cleveland shale (Up. Dev.). Sheffield, Ohio.
3949 NEWBERRY. *Pal. Fishes of N. Am., U. S. Geol. Surv.*, Mono. XVI, 1889,
3952 p. 165, Pl. XV, Figs. 1-5a.
- 15250 *Naiadites elongata* Dawson. Plesiotypes (2).
15251 Bear Run coal, Pottsville (Penn.). Elk Fork, Vinton Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 220,
Pl. XII, Figs. 7, 8.
- 15252 *Naiadites elongata* Dawson. Plesiotype.
Sharon ore, Pottsville (Penn.). Head of Higgins Run, Scioto
Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 220,
Pl. XII, Fig. 9.
- 15279 *Naiadites ohioense* Morningstar. Cotypes (3).
to Sharon ore, Pottsville (Penn.). Head of Higgins Run, Scioto
15281 Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 221,
Pl. XII, Figs. 10-13.
- 15310 *Naticopsis altonensis* (McChesney). Plesiotype.
Boggs limestone, Pottsville (Penn.). Near Hopewell P. O.,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 255,
Pl. XV, Fig. 15.
- 15169 *Naticopsis* (?) *diminuta* Stauffer and Schroyer. Cotypes (2).
15170 Base of Lower Washington limestone, Dunkard (Penn.).
One-half mile south of Pleasant Grove, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920,
p. 145, Pl. XI, Figs. 22, 23.
- 15311 *Naticopsis pulchella* Morningstar. Holotype.
Lower Mercer limestone, Pottsville (Penn.). Near East
Greenville, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 256,
Pl. XV, Fig. 16.
- 15243 *Naticopsis tortum* (Meek). Plesiotype.
McArthur limestone, Pottsville (Penn.). Elk Tp., Vinton
Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 257,
Pl. XV, Figs. 17, 18.
- 14030 *Nucula anodontoides* Meek. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 306, Pl. XIV,
Fig. 14.
- 15262 *Nucula elongata* Morningstar. Cotypes (2).
15263 Sharon ore, Pottsville (Penn.). Near mouth of Lick Run,
Scioto Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 201, Pl.
X, Figs. 10-13.
- 14029 *Nucula ventricosa* Hall. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 306, Pl. XIV,
Fig. 13.

- 15264 *Nuculopsis ventricosa* (Hall). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Near White Cottage, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 204, Pl. X, Fig. 20.
- 3208 *Nuculites* (*Cleidophorus*) *ferrugineum* Foerste.¹ Holotype.
Brassfield (Sil.). Todd's Fork, Wilmington, Ohio.
FOERSTE. *Geol. Surv. Ohio*, Vol. VII, 1893, p. 564, Pl. XXXVII, Figs. 2, 2b.
=*Clidophorus ferrugineus*.
- 14154 *Onychodus orton*i Newberry. Holotype.
Huron shale (Up. Dev.). Perry Tp., Franklin Co., Ohio.
NEWBERRY. *Pal. Fishes of N. Am.*, U. S. *Geol. Surv.*, Mono XVI, 1889, p. 71, Pl. XIX, Figs. 1, 1a.
- 3405 *Ophiodoceras wilmingtense* Foerste. Chiroholotype.
Niagaran (Sil.). Yellow Springs, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 15219 *Orbiculoidea stoutella* Morningstar. Cotypes (3).
to Harrison ore, Pottsville (Penn.). Hamilton Tp., Jackson Co., Ohio.
- 15221 Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 173, Pl. VII, Figs. 5-8.
- 4467 *Orthocanthus gracilis* Newberry. Holotype.
Upper Fremont limestone, Allegheny (Penn.). Linton, Ohio.
NEWBERRY. *Pal. Ohio*, Vol. II, 1875, p. 56, Pl. LIX, Fig. 7.
- 3428 *Orthoceras annulatum* Hall and Whitfield. Paratypes (9).
3432 Niagaran (Sil.). Cedarville, Yellow Springs, and Covington,
3499 Ohio.
HALL and WHITFIELD, *Pal. Ohio*, Vol. II, 1875, p. 147, Pl. 9, Fig. 1.
=*Dawsonoceras annulatum*.
- 3423A *Orthoceras crebescens* Hall and Whitfield (not Hall). Holotype.
Niagaran (Sil.). Cedarville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 148, Pl. IX, Fig. 2.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 545, Fig.
=*Orthoceras whitfieldi*.
- 4710 *Orthoceras isogramma* Meek. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge, Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 266, Pl. XVI, Fig. 5.
- 15239 *Orthoceras isogramma* Meek. Plesiotype.
Upper Mercer limestone, Pottsville (Penn.). Jefferson Tp., Coshocton Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 266, Pl. XVI, Fig. 6.

¹ In the description of this species Foerste states that the specimen was found on the same slab as *Cyrtodonta* (?) *ferruginea* (Hall and Whitfield) (see *Cypriocardites ferrugineum* of this catalogue); however, a careful examination of this piece of rock shows that the type is not present, and therefore must subsequently have been broken away. This entry is made because of the above reference by Foerste.

- 12217 *Orthoceras okawense* (?) Worthen. Plesiotype.
Maxville (Miss.). White Cottage, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911, p. 416, Fig. 36.
- 12216 *Orthoceras randolphense* Worthen. Plesiotype.
Maxville (Miss.). White Cottage, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911, p. 414, Fig. 35.
- 3423A *Orthoceras whitfieldi* Foerste mss. Chiroholotype.
Niagaran (Sil.). Cedarville, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
See *Orthoceras crebescens* Hall and Whitfield (not Hall).
- 2997 *Orthodesma contractum* (Hall). Plesiotype.
Cincinnatian (Ord.). Near Waynesville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 96, Pl. II, Figs. 4, 5.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 563, Figs.
- 2992 *Orthodesma curvatum* Hall and Whitfield. Paratypes (2).
Waynesville, Cincinnatian (Ord.). Waynesville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 95, Pl. II, Fig. 6.
- 9054 *Orthodesma rectum* Hall and Whitfield. Paratypes (2).
Waynesville, Cincinnatian (Ord.). Waynesville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 94, Pl. II, Figs. 7, 8.
- 14053 *Orthonema bilineatum* Mark. Holotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*. Fourth Ser., Bull. 17, 1912, p. 316, Pl. XVI, Fig. 14.
- 15332 *Orthonema subtaeniatum* Geinitz. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*. Fourth Ser., Bull. 17, 1912, p. 316, Pl. XVI, Fig. 3.
- 12212 *Orthonychia acutirostre* Hall. Plesiotype.
Maxville (Miss.). Cut 4, Mt. Perry-Fultonham, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911, p. 406, Fig. 30.
- 3238 *Palaeodictyota bella* (Hall and Whitfield). Holotype.
See *Inocaulis bella*.
- 15185 *Palaeoniscus* sp. Figured (2).
- 15186 Elm Grove limestone, Dunkard (Perm.). Raven Rocks, two miles north of Beallsville, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920, p. 146, Pl. XIII, Figs. 38, 39.
- 10422 *Paleschara beani* (James). Holotype.
See *Ceramopora* (?) *beani*.
- 15265 *Parallelodon obsoletus* (Meek and Worthen). Plesiotypes (2).
- 15266 Upper Pottsville (Penn.). Carbon Hill, Hocking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 205, Pl. XI, Figs. 1, 2.

- 14032 *Parallelodon tenuistriatus* (Meek and Worthen). Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 307, Pl. XV,
Fig. 2.
MORNINGSTAR. *Idem.*, Bull. 25, 1922, p. 210, Pl. X, Figs. 30, 31.
- 15305 *Patellostium montfortianum* (Norwood and Pratten). Plesiotype.
McArthur limestone, Pottsville (Penn.). Elk Tp., Vinton
Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 251,
Pl. XIV, Fig. 14.
- 5885 *Pentamerous oblongus* Sowerby. Plesiotype.
Niagaran (Sil.). Hillsboro, Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 2, 1895, p. 237, Pl. 67,
Fig. 20.
- 3364 *Pentamerous pergibbosus* Hall and Whitfield. Paratypes (10).
Niagaran (Sil.). Greenville and Rising Sun, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 139, Pl. VII, Figs.
10, 11.
- 3306 *Pentremites subcylindrica* Hall and Whitfield. Holotype and
Paratype.
Niagaran (Sil.). Yellow Springs, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 128, Pl. VI, Fig. 13.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 622, Fig.
- = *Troostocrinus subcylindricus*.
- 3298 *Periechocrinus ornatus* (Hall and Whitfield). Holotype and
Paratype.
See *Saccocrinus ornatus*.
- 8743 *Periechocrinus tennesseensis* (Hall). Paratypes (6).
- 3297 See *Saccocrinus tennesseensis*.
- 3379 *Phanerotrema occidens* (Hall). Plesiotype.
See *Pleurotomaria occidens*.
- 4592 *Pharkidonotus percarinatus* (Conrad). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 248,
Pl. XV, Fig. 6.
- 4701 *Phillipsia trinucleata* Herrick. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 274,
Pl. XVI, Fig. 9.
- 7302 *Phragmoceras aurora* Foerste mss. Chiroholotype and Chiro-
paratypes (3).
Niagaran (Sil.). Rising Sun, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 14809B *Phragmoceras aurora* Foerste. Chiroparatype.
Niagaran (Sil.). Bowling Green, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 10912 *Phragmoceras carmani* Foerste. Chiroholotype.
Niagaran (Sil.). Greene Co., Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.

- 9442A *Phragmoceras collicaire* Foerste. Chiroparatype.
Niagaran (Sil.). Bowling Green, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 3413 *Phragmoceras ellipticum* Hall and Whitfield. Holotype.
Niagaran (Sil.). Highland Co., Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 152, Pl. VIII, Fig. 11.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 637, Fig.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 3414 *Phragmoceras hillsboroense* Foerste. Chiroholotype.
Niagaran (Sil.). Highland Co., Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 5889 *Phragmoceras parvum* Hall and Whitfield. Holotype.
Niagaran (Sil.). Cedarville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 151, Pl. VIII, Fig. 10.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 9441A *Phragmoceras wilmingtontense* Foerste. Chiroparatype.
Niagaran (Sil.). Bowling Green, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 4609 *Placunopsis* (?) *reticardinalis* Meek. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 233, Pl.
XII, Fig. 19.
- 15341 *Plagioglypta prosseri* Morningstar. Cotype.
Lower Mercer limestone, Pottsville (Penn.). Near Fairview
School, Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 245,
Pl. XVI, Fig. 3.
- 4340 *Platycrinus bedfordensis* Hall and Whitfield. Holotype.
Upper Erie shale (Up. Dev.). Bedford, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 161, Pl. XIII, Fig. 4.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 686, Fig.
- 3316 *Platycrinus praematurus* Hall and Whitfield. Paratypes (18).
3323 Niagaran (Sil.). Cedarville and Greenville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 124, Pl. VI, Figs. 3-6.
= *Marsipocrinus praematurus*.
- 14038 *Pleurophorella geinitzi* (Meek). Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 240,
Pl. XIII, Figs. 18, 19.
See *Allerisma geinitzi*.
- 15294 *Pleurophorella sesquiplicata* Price. Plesiotypes (2).
15295 Lower Mercer limestone, Pottsville (Penn.). Rock Hollow,
Vinton Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 235,
Pl. XIII, Figs. 16, 17.
- 15303 *Pleurophorus immaturus* Herrick. Plesiotypes (2).
15328 Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 236, Pl.
XIV, Figs. 5, 7.

- 15302 *Pleurophorus immaturus* Herrick. Plesiotype.
McArthur limestone, Pottsville (Penn.). Elk Twp., Vinton Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 236, Pl. XIV, Figs. 6, 8.
- 14039 *Pleurophorus oblongus* Meek. Plesiotype.
Portersville limestone, Conemaugh (Penn.). Portersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 310, Pl. XV, Fig. 12.
- 15155 *Pleurophorus* (?) *ohioensis* Stauffer and Schroyer. Cotypes (2).
15156 Elm Grove limestone, Dunkard (Perm.). Two miles west of Martins Ferry, Ohio.
STAUFFER and SCHROYER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 22, 1920, p. 143, Pl. XI, Figs. 6, 7.
- 15248 *Pleurophorus spinulosa* Morningstar. Cotypes (2).
15249 Lower Mercer limestone, Pottsville (Penn.). Bald Knob, Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 239, Pl. XIV, Figs. 9-11.
- 15296 *Pleurophorus tropidophorus* Meek. Plesiotypes (2).
15297 Lower Mercer limestone, Pottsville (Penn.). Near Fairview School, Muskingum Co., and Flint Ridge, Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 240, Pl. XIII, Figs. 20, 21.
- 15242 *Pleurotomaria carbonaria* Norwood and Pratten. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge, Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 252, Pl. XV, Fig. 14.
- 3379 *Pleurotomaria occidentens* Hall and Whitfield. Plesiotype.
Niagaran (Sil.). Yellow Springs, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 142, Pl. VIII, Fig. 2.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 713, Fig.
= *Phanerotrema occidentens*.
- 15309 *Pleurotomaria ornatiformis* Morningstar. Cotypes (7).
Harrison ore, Pottsville (Penn.). Hamilton Twp., Jackson Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 253, Pl. XV, Figs. 7-13.
- 15274 *Posidonia girtyi* Morningstar. Cotypes (4).
to 4 Lower Mercer limestone, Pottsville (Penn.). Rock Hollow,
15277 Vinton Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 214, Pl. XII, Figs. 1-4.
- 15278 *Posidonia vintonensis* Morningstar. Cotypes (2).
Lower Mercer limestone, Pottsville (Penn.). Rock Hollow, Vinton Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 216, Pl. XII, Figs. 5, 6.

- 9888 *Poterioceras genuiflexum* Foerste mss. Chiroparatype.
Niagaran (Sil.). Highland Co., Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 5903 *Poterioceras genuiflexum* Foerste mss. Chiroholotype.
Niagaran (Sil.). Hillsboro, Ohio.
FOERSTE. *Manuscript on Silurian Cephalopoda*.
- 13295 *Productella hirsuta* Hall. Plesiotypes (2).
- 13298 Chagrin (Up. Dev.). Tinkers Creek, Bedford, Cuyahoga Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 547, Pl. XXXII, Figs. 8, 9.¹
- 13257 *Productella hirsuta* var. *rectispina* Hall. Plesiotypes (3).
- 13296 Chagrin (Up. Dev.). Brandywine Creek below Falls, Cuyahoga Co., Ohio.
- 13297 PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 542, Pl. XXXIII, Figs. 11-13.
- 12189 *Productus cestriensis* Worthen. Plesiotypes (7).
- 12190 Maxville (Miss.). Cut 6, Mt. Perry-Fultonham, and Kroft Bridge, White Cottage, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper 17, 1911, p. 372, Fig. 9.
- 15230 *Productus cora* D'Orbigny. Plesiotypes (3).
to Lower Mercer limestone, Pottsville (Penn.). Near Fairview
- 15232 School, Muskingum Co., and Flint Ridge, Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 180, Pl. VIII, Figs. 1-3.
- 14020 *Productus costatus* Sowerby. Plesiotype.
Cambridge limestone, Conemaugh (Penn.). Northup, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 302, Pl. XIII, Fig. 9.
- 14019 *Productus longispinus* Sowerby. Plesiotype.
Cambridge limestone, Conemaugh (Penn.). Norwich, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 302, Pl. XIII, Fig. 8.
=*Marginifera wabashensis*.
- 14018 *Productus pertenuis* Meek. Plesiotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 303, Pl. XIII, Fig. 7.
=*Pustula pertenuis*.
- 12188 *Productus pileiformis* McChesney. Plesiotypes (3).
Maxville (Miss.). White Cottage, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Special Paper 17, 1911, p. 370, Figs. 8a-c.
- 14017 *Productus punctatus* (Martin). Plesiotype.
Cambridge limestone, Conemaugh (Penn.). Cambridge, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 303, Pl. XIII, Fig. 6.
=*Pustula punctatus*.

¹ The specimen shown in Fig. 7 is not in this collection.

- 15233 *Productus semireticulatus* (Martin) var. Figured (2).
15234 Lower Mercer limestone, Pottsville (Penn.). Symmes Creek,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 181,
Pl. VIII, Figs. 4, 5.
- 9823 *Productus semireticulatus* (Martin). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Blunt Run,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 181,
Pl. VIII, Fig. 6.
- 15214 *Prismopora sereata* (Meek). Plesiotype.
McArthur limestone, Pottsville (Penn.). Elk Tp., Vinton Co.,
Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 165,
Pl. VI, Fig. 21.
- 4210 *Promacrus andrewsi* Meek. Holotype.
Waverly (Miss.). Sciotoville, Ohio.
MEEK. *Pal. Ohio*, Vol. II, 1875, p. 308, Pl. 17, Figs. 1a, b.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, pp. 772, 773, Figs.
- 15304 *Prothyris elegans* Meek. Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 195,
Pl. XIV, Fig. 12.
- 10421 *Ptilodictya flagellum* Nicholson. Holotype.
Richmond (Ord.). Lebanon, Ohio.
NICHOLSON. *Am. Mag. Nat. Hist.*, Fourth Ser., 15, 1875, p. 179, Pl. XIV,
Figs. 3-3b.; *Pal. Ohio*, Vol. II, 1875, p. 262, Pl. 25, Figs. 4-4b.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 827, Figs.
- 3292 *Ptiloporella nervata* (Nicholson). Holotype.
See *Fenestella nervata*.
- 14023 *Pugnax utah* (Marcou). Plesiotypes (2).
Ames limestone, Conemaugh (Penn.). Steubenville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 303, Pl. XIV,
Figs. 3, 4.
- 14018 *Pustula pertenuis* (Meek). Plesiotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 183, Pl.
VIII, Fig. 8.
See *Productus pertenuis*.
- 14017 *Pustula punctatus* (Martin). Plesiotype.
Cambridge limestone, Conemaugh (Penn.). Cambridge, Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 183,
Pl. VII, Fig. 9.
See *Productus punctatus*.
- 14905 *Receptaculites ohioensis* Hall and Whitfield. Paratype.
Niagaran (Sil.). Yellow Springs, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 123, Pl. VI, Fig. 1.

- 13299 *Reticularia praematura* (Hall) Schuchert. Plesiotypes (2).
13300 Chagrin (Up. Dev.). Two miles east of Trumbull Center,
Trumbull Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 535, Pl. XXIX,
Figs. 7, 8.
- 3513 *Retsia formosa* Whitfield (not Hall). Cotype.
Greenfield dolomite, Monroe (Sil.). Greenfield, Ohio.
WHITFIELD. *Ann. New York Acad. Sci.*, Vol. V, 1891, p. 512, Pl. V, Fig.
16; *Geol. Surv. Ohio*, Vol. VII, 1893, p. 413, Pl. I, Fig. 16.
SHERZER. *Geol. Surv. Mich.*, Vol. VII, Pt. 1, 1900, p. 224, Pl. XVII,
Fig. 16.
= *Rhynchospira praeformosa*.
- 14021 *Rhipidomella pecosi* (Marcou). Plesiotype.
Ames limestone, Conemaugh (Penn.). Deersville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 303, Pl. XIII,
Fig. 10.
MORNINGSTAR. *Idem.*, Bull. 25, 1922, p. 175, Pl. VII, Fig. 13.
- 4500 *Rhizodus lancifer* Newberry. Holotype.
Upper Freeport limestone, Allegheny (Penn.). Linton, Ohio.
NEWBERRY. *Proc. Acad. Nat. Sci. Phil.*, loc. cit.; *Pal. Ohio*, Vol. I,
1873, p. 342, Pl. 39, Fig. 9.
LESLEY. *Geol. Surv. P. Pa.*, P. 4, 1889, p. 876, Fig.
- 3515 *Rhynchonella hydraulica* Whitfield. Holotype.
Greenfield dolomite, Monroe (Sil.). Greenfield, Ohio.
WHITFIELD. *Ann. New York Acad. Sci.*, Vol. II, 1882, p. 194; *Idem.*, Vol.
V, 1891, p. 512, Pl. V, Fig. 17; *Geol. Surv. Ohio*, Vol. VII, 1893,
p. 414, Pl. I, Fig. 17.
SHERZER. *Geol. Surv. Mich.*, Vol. VII, Pt. 1, 1900, p. 128, Pl. XVII,
Fig. 17.
= *Camarotoechia hydraulica*.
- 3513 *Rhynchospira praeformosa* Grabau. Cotype.
Greenfield dolomite, Monroe (Sil.). Greenfield, Ohio.
GRABAU. *Geol. Surv. Mich.*, Ser. 1, 1909, p. 131, Pl. XXX, Fig. 16.
See *Retzia formosa*.
- 3298 *Saccocrinus ornatus* Hall and Whitfield. Holotype and Paratype.
Niagaran (Sil.). Yellow Springs, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 126, Pl. VI, Figs. 7-9.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 917, Figs.
= *Periechocrinus ornatus*.
- 8743 *Saccocrinus tennesseensis* Hall and Whitfield. Paratypes (6).
3297 Niagaran (Sil.). Yellow Springs, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 125, Pl. VI, Fig. 10.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 917, Fig.
= *Periechocrinus tennesseensis*.
- 15285 *Schizodus affinis* Herrick. Plesiotype.
McArthur limestone, Pottsville (Penn.). Monroe Furnace,
Jackson Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 223, Pl.
XII, Fig. 17.

- 15247 *Schizodus amplus* Meek and Worthen. Plesiotype.
Boggs limestone, Pottsville (Penn.). Near Hopewell, P. O.,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 222,
Pl. XII, Fig. 18.
- 4591 *Schizodus cuneatus* Meek. Plesiotypes (2).
Lower Mercer limestone, Pottsville (Penn.). Flint Ridge,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 223,
Pl. XIII, Figs. 1, 2.
- 15282 *Schizodus subcircularis* Herrick. Plesiotypes (3).
to McArthur limestone, Pottsville (Penn.). Monroe Furnace,
15284 Jackson Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 225,
Pl. XII, Figs. 14-16.
- 15244 *Schizostoma catilloides* (Conrad). Plesiotypes (2).
McArthur limestone, Pottsville (Penn.). Elk Tp., Vinton
Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 255, Pl.
XV, Figs. 19, 20.
- 3512 *Schuchertella hydraulica* (Whitfield). Cotypes (2).
Greenfield dolomite, Monroe (Sil.?). Greenfield, Ohio.
GRABAU. *Geol. Surv. Mich.*, Geol. Ser. 1, 1909, p. 120, Pl. 30, Figs. 1-3.
See *Streptorhynchus hydraulicum*.
- 14058 *Soleniscus aplatus* Mark. Holotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 318, Pl. XVI,
Fig. 19.
- 14057 *Soleniscus brevis* White. Plesiotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 318, Pl. XVI,
Fig. 18.
=*Sphaerodoma ventricosa* (Hall), not *Sphaerodoma brevis*
(White).
- 14056 *Soleniscus paludinaeformis* (Hall). Plesiotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 317, Pl. XVI,
Fig. 17.
=*Sphaerodoma paludinaeformis*.
- 14055 *Soleniscus typicus* Meek and Worthen. Plesiotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 317, Pl. XVI,
Fig. 16.
- 15255 *Solenomorpha lamborni* Morningstar. Cotypes (2).
Sharon ore, Pottsville (Penn.). Near mouth of Lick Run,
Scioto Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 195,
Pl. X, Fig. 3.

- 15245 *Solenomya* (?) *sharonensis* Morningstar. Holotype.
Sharon ore, Pottsville (Penn.). Near mouth of Lick Run,
Scioto Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 195,
Pl. X, Figs. 1, 2.
- 15312 *Sphaerodoma brevis* (White). Plesiotype.
McArthur limestone, Pottsville (Penn.). Elk Tp., Vinton Co.,
Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 261,
Pl. XV, Fig. 22.
- 15313 *Sphaerodoma brevis* (White). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Near East
Greenville, Stark Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, P. 261,
Pl. XV, Figs. 23, 24.
- 14056 *Sphaerodoma paludinaeformis* (Hall). Plesiotype.
See *Soleniscus paludinaeformis*.
- 14057 *Sphaerodoma ventricosa* (Hall). Plesiotype.
See *Soleniscus brevis*.
- 15321 *Spirifer boonensis* Swallow? Plesiotypes (5).
to Boggs limestone, Pottsville (Penn.). Near Hopewell P. O.,
15324 Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 186, Pl.
IX, Figs. 21-25.
- 14022 *Spirifer cameratus* Morton. Plesiotype.
Cambridge limestone, Conemaugh (Penn.). Langsville, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 304, Pl. XIV,
Figs. 1, 2.
MORNINGSTAR. *Idem.*, Bull. 25, 1922, p. 188, Pl. IX, Figs. 11, 12.
- 13301 *Spirifer disjunctus* Sowerby. Plesiotypes (3).
to Chagrin (Up. Dev.). Brandywine Creek below Falls, Cuy-
13303 ahoga Co., Ohio.
PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 534, Pl. XXIX,
Figs. 3-6.
- 15325 *Spirifer opimus* Hall. Plesiotypes (8).
to Upper Pottsville (Penn.). Carbon Hill, Hocking Co., Ohio.
15326 MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 188,
Pl. IX, Figs. 13-20.
- 10356 *Spiriferina kentuckyensis* (Shumard). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Union Furnace,
Vinton Co., Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 2, 1894, p. 51, Pl.
XXIX, Fig. 17.
- 15212 *Streblotrypa merceri* Morningstar. Holotype.
Lower Mercer limestone, Pottsville (Penn.). Bald Knob,
Licking Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 164, Pl.
VI, Figs. 16, 17.

- 3512 *Streptorhynchus hydraulicum* Whitfield. Cotypes (2).
Greenfield dolomite, Monroe (Sil.?). Greenfield, Ohio.
WHITFIELD. *Ann. New York Acad. Sci.*, Vol. II, 1882, p. 193; *Idem.*,
Vol. V, 1891, p. 508, Pl. V, Figs. 1-3; *Geol. Surv. Ohio*, Vol. VII,
1893, p. 410, Pl. I, Figs. 1-3.
SHERZER. *Geol. Surv. Mich.*, Vol. VII, Pt. 1, 1900, Pl. XVII, Figs. 1-3.
= *Schuchertella hydraulica*.
- 10419 *Stromatopora scabra* James. Holotype.
Cincinnati (Ord.). Lebanon, Ohio.
JAMES. *Paleontologist*, 3, 1879; *Jour. Cinci. Soc. Nat. Hist.*, Vol. IX,
1886, p. 251; *Idem.*, 1892, p. 91.
= *Dermatostroma scabrum*.
- 13304 *Strophalosia muricata* (Hall). Plesiotypes (4).
to Chagrin (Up. Dev.). Crooked Creek, Ashtabula Co., Ohio.
- 13307 PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 542, Pl. XXXII,
Figs. 10-13.
- 12213 *Strophostylus carleyana* Hall. Plesiotype.
Maxville (Miss.). Cut 4, Mt. Perry-Fultonham, Ohio.
MORSE. *Proc. Ohio Acad. Sci.*, Vol. V, Pt. 7, Special Paper, 17, 1911,
p. 408, Fig. 31.
- 3743 *Stylasteria anna* Whitfield. Paratypes (3).
Columbus limestone (Dev.). Antwerp, Ohio.
WHITFIELD. *Ann. New York Acad. Sci.*, Vol. II, 1882, p. 199; *Idem.*,
Vol. V, 1891, Pl. VI, Figs. 1-5; *Geol. Surv. Ohio*, Vol. VII, 1893, p.
420, Pl. II, Figs. 1-5.
= *Acervularia davidsoni*.
- 3390 *Subtulites terebriformis* Hall and Whitfield. Holotype.
Niagaran (Sil.). Clifton, Greene Co., Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 141, Pl. 8, Fig. 6.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 1143, Fig.
- 15317 *Squamularia perplexa* (McChesney). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Blunt Run,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 191,
Pl. IX, Figs. 26, 27.
- 13308 *Syringothyris texta* var. *chemungensis* Cushing. Plesiotypes (4).
- 13312 Chagrin (Up. Dev.). Mill Creek, north of Jefferson, Ashtabula
to Co., Ohio.
- 13314 PROSSER. *Geol. Surv. Ohio*, Fourth Ser., Bull. 15, 1912, p. 537, Pl. XXXI,
Figs. 1-5.
- 15201 *Textularia* sp. Figured (2).
Upper Mercer flint, Pottsville (Penn.). Near Rock Cut,
Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 152,
Pl. VI, Figs. 1, 2.
- 3376 *Trimerella grandis* Billings. Plesiotype.
Niagaran (Sil.). Near Sinking Springs, Highland Co., Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 1, 1892, Pl. 4A, Figs.
1, 2.

- 9009 *Trimerella ohioensis* Meek. Plesiotype.
Niagaran, Guelph (Sil.). Genoa, Ottawa Co., Ohio.
HALL and CLARKE. *Pal. New York*, Vol. VIII, Pt. 1, 1892, Pl. 4A,
Figs. 5, 6.
- 9003 *Triplecia ortonii* (Meek). Cotype.
Top of Brassfield (Sil.). Near Dayton, Ohio.
MEEK. *Geol. Surv. Ohio*, Vol. I, 1873, p. 178, Pl. XV, Fig. 1f.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 1226, Fig.
See *Dicraniscus ortonii*.
- 3380 *Trochonema pauper* var. *ohioensis* Hall and Whitfield. Holotype.
Niagaran (Sil.). Greenville, Ohio.
HALL and WHITFIELD. *Pal. Ohio*, Vol. II, 1875, p. 143, Pl. 8, Fig. 4.
LESLEY. *Geol. Surv. Pa.*, P. 4, 1889, p. 1230, Fig.
- 3306 *Troostocrinus subcylindricus* (Hall and Whitfield). Holotype and
Paratype.
Niagaran (Sil.). Yellow Springs, Ohio.
FOERSTE. *Ohio Jour. Sci.*, Vol. XXI, No. 2, Dec., 1920, p. 65, Pl. III,
Figs. 3a, b.
See *Pentremites subcylindrica*.
- 3024 *Whiteavesia cincinnatiensis* (Hall and Whitfield). Cotype.
See *Modiolopsis cincinnatiensis*.
- 2988 *Whitella ohioensis* Ulrich. Holotype.
Cincinnatian (Ord.). Waynesville, Ohio.
ULRICH. *Geol. Surv. Ohio*, Vol. VII, 1893, p. 678, Fig. 2.
- 14043 *Worthenia beedei* Mark. Holotype.
Ames limestone, Conemaugh (Penn.). New Concord, Ohio.
MARK. *Geol. Surv. Ohio*, Fourth Ser., Bull. 17, 1912, p. 312, Pl. XVI,
Fig. 1.
- 15315 *Zygopleura plenum* (Herrick). Plesiotype.
Lower Mercer limestone, Pottsville (Penn.). Near Fairview
School, Muskingum Co., Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 258,
Pl. XVI, Fig. 1.
- 15316 *Zygopleura plenum* (Herrick). Plesiotype.
McArthur limestone, Pottsville (Penn.). Elk Tp., Vinton Co.,
Ohio.
MORNINGSTAR. *Geol. Surv. Ohio*, Fourth Ser., Bull. 25, 1922, p. 258,
Pl. XVI, Fig. 2.

Received for publication November 27, 1923.

THE OHIO JOURNAL OF SCIENCE

VOL. XXIV

MARCH, 1924

No. 2

A PHYSIOLOGICAL STUDY OF GROWTH AND REPRODUCTION AMONG CERTAIN GREEN ALGAE.*†

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INTRODUCTION.

Within the last decade or two the algæ have assumed a position of increasing importance because of their relation to aquatic animals, particularly the fishes. There can be no question that for the most part fishes are dependent upon the algæ as direct or indirect sources of their food and energy. The writer (34) has previously called attention to the present and future possibilities of the algæ as indirect sources of food and energy for the human race through the game fishes. The time may speedily come when fishes shall be more generally used as human food, than at present.

It appears, therefore, that any study which increases our knowledge of the fundamental processes and structures of the algæ not only gives us a better conception of the plant kingdom in general but also is a stepping stone toward a scientific cultivation of these plants for fishes.

In reviewing literature on the physiology of the algæ, one notes that two kinds of investigations have been carried on to ascertain (a) the effect of environmental changes on variations in growth and reproduction, and to a smaller degree (b) the nature and kind of substances composing cell walls, protoplasts, stored foods, and pyrenoids. There remains a rather important phase of the subject to extend and correlate these two kinds of work, and to discover what are the actual changes that take

* A thesis presented in partial fulfillment of the requirements for the Degree of Doctor of Philosophy in the Graduate School of The Ohio State University.

† Papers from the Department of Botany, The Ohio State University, No. 143.

place in the alga from germination to spore production. For the last three years the writer has made some attempt to correlate, as far as possible, the interrelations of the vegetative and reproductive phases of some of the green algæ with related physiological processes and the changes in the factors of the environment that affect them.

For the sake of ease and clarity of presentation, the results of this work are here recorded under five divisions. It will be convenient, however, to mention some of the work of previous investigators directly in connection with the results of my own work, somewhat regardless of these five major divisions:

- I. Review of literature.
- II. The cell walls: nature, formation, and variation during growth and reproduction.
- III. Protoplasmic inclusions of the nature of food reserves.
- IV. Mineral salts.
- V. Some environmental factors and their effect on II, III, and IV.

I.

REVIEW OF LITERATURE.

European and American workers have been interested for a number of years in the forms assumed by the green algæ during vegetative development and the initiation of reproductive activities. Their investigations, for the most part, have consisted in calling attention to the various phenomena of reproduction among the algæ and in ascertaining the correlative environmental changes, causative or coincidental.

Pringsheim (29) as early as 1860 had noted that the cell produced by a zoospore among certain Ulothrichales may produce other zoospores immediately upon the attainment of full size, or earlier; or it may pass through a quiescent stage before germination.

Klebs (18) in 1896 observed that *Stigeoclonium tenue* produced round rather than elongated cells in concentrated solution of Knop's nutritive medium. The same author made extensive observations on various species of *Vaucheria*, *Hydrodictyon*, *Spirogyra*, and *Draparnaldia* to ascertain the effect upon sexual and non-sexual reproduction of such conditions as nutrition, moisture, light, temperature, chemical composition

of the medium, and oxygen. In some species it was possible to produce either sex organs or zoospores almost at will and to produce predominately one or the other. In other species, however, no changes could be effected artificially.

Livingston (22) in 1900 in growing a species of *Stigeoclonium* in Knop's solution came to the conclusion that variations in the form of this alga were due to variations in osmotic pressure of the medium, independent of the chemical nature of the salts. He says that a high osmotic pressure in the external medium means (a) decreased vegetative activity, (b) an inhibition of zoospore production, (c) a change from cylindrical to spherical cells, and (d) allows for the plane of cell division to be less restricted. A year later the same author (23) explained the change in state from cylindric to spherical cells as being due to changes in water content of the cells; further, that such polymorphism is not related to the photosynthetic process; *i. e.*, darkness has no effect, one way or the other.

A few years later Artari (1) and Matruchot and Molliard (25) found that *Stichococcus bacillaris* in strong sugar solutions produced long, twisted cells, in filaments; in weak solutions there occurred short thick cells, usually isolated. Thus, diametrically opposite results are secured with *Stigeoclonium* and with *Stichococcus*, when grown in media of low and high osmotic pressure.

In 1900 Pierce and Randolph (28) working in Italy on "irritability in algæ" observed that the degree of roughness and the character of the surface with which zoospores come into contact determined the extensiveness of holdfast development subsequent to germination; that even among the so-called "non-attached algæ" holdfasts may form if the proper "contact stimulus" be supplied. The authors conclude (a) that the zoospores of *Oedogonium* come to rest more as a response to the intensity and direction of light than to any other factors; (b) that germination of the zoospores is induced primarily by an interference with their locomotion; (c) that forms and extensiveness of attachment (holdfasts) are determined by the roughness of the surface with which the zoospores come into contact; and (d) that the direction of the growth of rhizoids is always negatively phototropic. Fritsch (10) a little later reported that the zoospores of *Oedogonium capillare* sometimes germinated before actually coming to rest.

Rayss (30) made extensive studies of *Cœlastrum proboscideum* to determine the environmental factors related to changes in state of that alga. He observed that *Cœlastrum* under normal conditions produced cœnobes. With increasing concentration of nutrient media, isolation of the cells of the alga occurred; abundant nutrition meant large cells and large numbers of cells in the cœnobe; lack of oxygenation caused disarticulation of the cells in the cœnobe; abundant oil formation resulted if the medium were peptone; calcium salts in the proportion of .25 to 1.75 per cent greatly favored the production of cœnobias, while salts of potassium of a similar concentration inhibited cœnobic development; an alkaline medium seemed most favorable to the development of this species of *Cœlastrum*.

From another point of view several investigators have recorded results of chemical investigations upon the nature of the cell wall and of the protoplast of the green algæ.

West (41, 42) says the cell walls of most green algæ are made of cellulose, sometimes largely of pectose; in all cases that the wall is a secretion of the protoplasm arising on the outer surface of the protoplast. Sometimes cellulose and pectose are sharply differentiated, either in distinct layers or not. The cellulose compounds are usually very compact, surrounded by the gelatinized pectic compounds. Careful investigation by West and Hood (43) shows that *Trentopohlia*, an alga related to *Ulothrix*, has an apical cap composed entirely of pectose. The cell walls are lamellose, and the lamellæ are cellulose. Virieux (40) in 1910 found evidence of callose in the mucilage of certain *Chlorophyceæ*. Lemaire (20) records schizophycose in the sheaths of the *Stigonemaceæ*. Crow (8) thinks that cell membranes of algæ differ in some ways from those of the higher plants.

According to Lemmermann (21), cellulose occurs in greater or less amounts in all cell walls and goes into solution in concentrated sulphuric acid and in copperoxide-ammonia. This author gives numerous color tests for pectin, starch, sugars, proteins, fats, and oils found in the algæ.

Oltmanns (27) records that of all cell walls those of the algæ are the most variable. He does not believe that the "cuticle" of the *Zygnemaceæ* is identical with that of higher plants, but assigns no reason for his position. Upon plasmolysis, the protoplasts of *Zygnema* secrete a new membrane around the contracted protoplasm, supposedly of cellulose.

Hirn (15) described the formation of the so-called apical caps in *Oedogonium* by the development of a circular ring of cellulose just within the upper extremity of the cell, which upon enlargement, ruptures the old wall, forming a ring at the apex as cell division occurs. The author made an attempt to control this development experimentally.

Hodgett (16) described a new species of *Spirogyra* with peculiar rod-shaped structures in the cell walls at right angles to the length of the filament. He did not discuss their formation, structure, or significance. Similar structures have been noted in *Spirogyra submaxima* by Transeau.

In the formation of zygospores and aplanospores in the genus *Debarya*, Transeau (36) records the presence of pectic materials within the gametangia surrounding the spores. The same author notes a pectose sheath of seventeen microns thickness in *Spirogyra submaxima*. Transeau (37) has further studied reproduction in *Spirogyra illinoiensis* and notes that "conjugation is initiated by the bending of the gametangia and the development of slight prominences on both cells. This is followed by a mucilaginous secretion at the point of contact, which may persist as a ring about the tube for several days after the union of the cells is complete. After contact, the chromatophores become gorged with starch and fatty bodies, the enlargement of the cell continues, but stops in the case of the male cell when the gamete passes over."

Some very interesting studies of the Myxophyceæ have been made by such workers as Lemaire (20), Griffiths (12), Crow (8), and Mameli (24). The blue-green algæ resemble the greens in some ways, but in others are markedly different. The writer has in progress some investigations on this group of algæ, which will appear in a subsequent paper.

II.

THE CELL WALLS.

1. *Methods of Attack.*

It has been repeatedly stated by various authors that the constituent materials of cell wall membranes among the algæ were in some manner different from those of the cells in the higher plants. Such expressions as "fungus-cellulose," "chitin-cellulose," and "schizophycose" are indicative of a feeling on

the part of the investigator that such substances have peculiar chemical or physical properties unlike the ordinary substances found in plants. Cell walls vary considerably in the degree and ease of solubility of their constituent parts as well as in permeability to chemical reagents. Wurdack (44), working in this laboratory, found that after removing the outer chitinous layer of *Cladophora glomerata*, the ordinary tests for pectose and cellulose could readily be made. Many of the larger Zygnemaceæ can be immersed in copperoxideammonia for weeks with apparently no change in the cellulose membranes. After treatment for the removal of the pectose layer, however, the cellulose is dissolved in a very few minutes, sometimes almost instantaneously, in the same reagent. The middle wall of the spores of certain species of Spirogyra has deposits of chitin, and this greatly lengthens the time required for the cellulose of this layer to go into solution. After the removal of the chitin, the cellulose dissolves readily. It would seem, then, that the difficulty of ascertaining the nature of the cell walls in the green algæ lies not in the presence of peculiar compounds of strange chemical composition, but rather in the presence of layers of different membrane substances.

Color reactions are not always satisfactory, on the whole, with the majority of algæ unless cross sectioned material is available. The cells of most filamentous algæ are cylinders with the layers in the cell walls one outside the other, and color restrictions to definite areas cannot be detected with any degree of certainty. Solubility tests are most reliable either directly or upon crystals of precipitation. Among the higher plants, if both pectic compounds and cellulose are present, either may be dissolved leaving the other intact. In the species of Zygnemaceæ studied, it is absolutely necessary that the outer layer of pectose be first removed; otherwise, as noted above, the impermeability of the pectose prevents the cellulose-dissolving reagent from coming into contact with the cellulose, or else allows only slight diffusion through itself.

Algæ preserved in 6-3-1* are readily available for most microchemical analyses. A comparison of the same species of Mougeotia, Zygnema, and Spirogyra after being kept in this preservative for a number of years with the freshly collected

* Six parts water, three parts 95% alcohol, and one part formalin.

material showed practically the same reactions toward chemical tests. It must be borne in mind, however, that as a rule preserved material reacts more slowly both as regards solubility and color reactions; otherwise no differences could be discerned. If pectic acid form the larger part of the gelatinous matrix, as for example in some stages of *Tetraspora* and *Palmodictyon*, the material undergoes considerable dissolving in the preservative. To be able to correlate the nature of compounds, as well as the amounts, with the growth of the alga, it is desirable to have freshly collected material.

In my work upon the cell walls of certain green algæ the standard microchemical tests have been used. With restrictions and modifications noted above, the order recommended by Tunmann (39) is good:

- a. Color reactions.
- b. Solubility.
- c. Hydrolysis and tests for hydrolytic products.
- d. Precipitation.
- e. Crystal formation.
- f. Optical properties.

Since the membrane materials are often delicate and deposited in small quantities, it is quite essential that the investigator "be on hand" when the reactions are taking place. The cell walls of *Microspora Willeana* under polarized light are almost wholly bright, due to the prominence of the cellulose. If copperoxideammonia be applied, the cellulose may swell to such an extent as to burst the pectose layer on the outside, later dissolving. One might conclude that the cell membrane contained nothing but cellulose. The middle layer of the spores of many of the Zygnemaceæ will after a time disappear in copperoxideammonia, but if one notes the difficulty of solubility and applies other tests, he finds deposits of chitin.

It should also be emphasized that tests must be repeated many times if one's conclusions are to be really conclusive. A filament of *Tribonema bombycina* when placed in dilute potassium hydroxide was observed to "peel off" layer by layer and go into solution—pectic acid. Other filaments in warm 2% hydrochloric acid followed by 2% potassium hydroxide disappeared entirely, but were unaffected by the potassium hydroxide alone—pectose. Still other filaments were observed to

disintegrate slowly and imperfectly into H-pieces and finally dissolve in copperoxideammonia—cellulose. If one were to take these tests separately and alone he would find the membrane in one case to be pectic acid, in another pectose, and in still another cellulose. This variation is somewhat a matter of age, the older filaments having relatively less pectic compounds and a greater amount of cellulose.

By the use of a small piece of blotting paper adjacent to one side of the cover glass, it is possible to get reactions of a single alga to various reagents which can be "drawn through" from the other side of the cover glass, one after the other. This not only saves time, but makes it possible for one to observe all the changes in the individual alga and to be assured it is the same alga under continuous observation.

In the selection of material for experimental work it was necessary to pay considerable attention to those species of algæ which were accessible at various seasons of the year. To get fresh specimens in the winter time, recourse was had to those forms growing in water tanks in the botany greenhouse. Most of the algæ used are common in Ohio. This report does not attempt to give complete analyses of any group or groups of algæ, neither does it strive to point out relationships among these groups, as such. The aim has been to select individuals representing essentially diverse taxonomic categories among the Chlorophyceæ, thus laying the foundation for more specific work among certain groups or genera at a later time.

2. *The Zygnemaceæ.*

The Zygnemaceæ are represented in Ohio by four distinct genera—Mougeotia, Debarya, Zygnema, and Spirogyra—differing from each other chiefly in the nature of the protoplast and in the method of reproduction. The family is world-wide and constitutes some of our commonest freshwater algæ. The thallus is filamentous, consisting of a single series of cells that form an unbranched filament. The nature of the cell walls and notes on growth and reproduction of these algæ follow under each genus.

a. *Mougeotia.*

In the genus Mougeotia the cell wall in the vegetative state is entirely of cellulose, surrounded by a thin mucilaginous

investment which is, in all cases studied, of pectose. In weak hydrochloric acid warmed over a water bath for twenty to thirty minutes, followed by warm alkalies, the pectose is easily soluble. When the pectose layer is removed, the cellulose membrane dissolves away very readily upon the application of copperoxideammonia or 60% sulphuric acid. On the other hand, if freshly collected material be subjected to treatment with copperoxideammonia, several hours are usually required for the penetration of the pectose layer by the reagent. Material preserved in 6-3-1 must first be treated for the removal of the pectose layer before copperoxideammonia will penetrate through the pectose to the cellulose. Filaments of *Mougeotia robusta* in the copperoxideammonia for five weeks were unaffected.

The middle lamella formed from the first transverse division laid down in the cell is pectose. Just previous to fragmentation of the filament the lenticular area of pectose becomes pectin, which upon dissolving leads to the separation of the adjacent cells at the plane of the original lamella. This fragmentation may occur between all the cells of the filament, or irregularly throughout the thallus.

The formation of zygospores in *Mougeotia* from only a part of the protoplast of the gametangium institutes wall formation peculiar to the genus. Partition walls of cellulose cut off the zygospore from the rest of the gametangium, and later other membrane layers are deposited within the first partition. These differentiated layers are the wall of the zygospore. The outer layer, which is the first one formed, and the inner layer are of cellulose. The middle layer (sometimes layers) is usually quite distinct from the other two. It is usually isotropic in polarized light, insoluble in weak acids, and very difficultly soluble in copperoxideammonia. Concentrated chlorzinciodide causes the appearance of a faint violet color in the membrane, finally disappearing. The red-violet color indicating chitosan is usually clear, sometimes very definite, and occasionally lacking. These phenomena indicate that the middle layer is not pure cellulose but contains deposits of chitin. There is no evidence of a definite chitinous layer, but the amount of chitin present may vary from none at all to a considerable quantity. The amount of chitinous deposits varies not only with the different species examined, but in the spores of the same filament. It is interesting to note that the markings of the spore wall, whose presence

or absence is often an ultimate criterion of species identification, are present only on this middle layer. The warts of the spores of *Mougeotia quadrangulata* are cellulose with varying amounts of chitin.

Mougeotia genuflexa exhibits a peculiar "contact-formation" between cells of the filaments that causes the amateur much fruitless search for the zygospores supposedly appearing subsequent to this apparent conjugation. Accompanying the genuflexing is the separation of the "knee-joints" from the rest of the filament by the formation of soluble pectin at the region of the middle lamella. Actual communication apparently does not result from such contact, although stages are common in which the appressed walls are completely fused into one. Nieuwland (26) thinks that this occurrence is merely a step in the process of vegetative multiplication. Kneeing is probably the result of changes in the chemical nature of the cell wall accompanied by internal pressure. There is a rapid increase in the amount of pectose at the region of the "bulge," and when these pectose areas from different filaments come into contact, the two knees are "glued" together. Oftentimes the cellulose layers never come into actual contact, being separated by the pectose layer; sometimes the cellulose layers come into contact, but never fuse; or there may be complete fusion, the appressed region acting as one cell wall. In some cases, particularly when the alga is growing in a 5% solution of sucrose, there occurs a breaking up of the protoplasm and a movement of the disintegrated protoplasts towards the points of contact. Nothing nearer than this to actual fusion of gametes was ever observed, and further movement could not be induced artificially.

The above report regarding the genus *Mougeotia* is based on a study of the following species: *Mougeotia quadrangulata*, *M. robusta*, *M. robusta biornata*, *M. calcarea*, and *M. genuflexa*.

b. *Debarya*.

In the genus *Debarya* the zygote is the result of the fusion of gametes formed from the entire contents of the gametangia. Chemically the walls of the vegetative cells are identical with those of *Mougeotia* and *Zygnema*. West (41) in describing the formation of the zygospore speaks of the laying down of a series of cellulose layers resulting in a much thickened gametangial wall. In *Debarya decussata* this is accompanied by

deposits of chitin. The highly refractive area formed in the gametangia upon the maturing of the zygospores has been supposed to be of pectic compounds. Careful investigation upon the filaments of *D. decussata* failed to show any pectic compounds in this area, but the cellulose tests were positive. Further work is desirable on other species of this interesting genus.

c. Zygnema.

The genus *Zygnema* is very similar chemically to *Mougeotia* and *Debarya*. The external pectose sheath in *Z. pectinatum* may reach a thickness of nine microns. The cells of the filaments of *Zygnema* are usually shorter and thicker than those of the two genera mentioned above. The spores are formed from the entire contents of the gametangia and consist of three wall layers, all of cellulose with the middle one often chitinized.

As reproduction is initiated in *Zygnema* it not infrequently happens that there is incomplete fusion of the gametes in zygospore formation, and two "spores" result. In some species of the genus, aplanosporic formation is common. In either of these cases the spore walls are formed in the same way as in the ordinary zygote. Upon plasmolysis, either natural or induced artificially, the protoplast secretes a new wall of cellulose within the old cell wall.

In *Z. insignis* the mature zygospores have deposits of chitin in the middle layer and the outer spore membrane is often entirely of pectose. Other species with chitinous deposits in the middle spore membrane are *Z. stellinum*, *Z. pectinatum*, *Z. collinsianum*, and *Z. decussatum*.

Hodgett (17) has made careful observations of the conjugation of *Zygnema* (*Zygonium*) *ericetorum*, which in some ways resembles that of *Spirogyra majuscula*, noted below. He says that cells of adjacent filaments put out protuberances that meet and become flattened against each other, mucilage being developed from the outermost layers of the cell walls. The protuberances are due to the more active growth of the innermost layer, the outgrowth being thickened by deposition of new internal layers of cellulose. The alga exhibits a rather unique peculiarity prior to the fusion of the gametes in that a thin wall of cellulose forms around each gamete. Later, the line of separation between the two gametes is lost, fusion occurs,

and an ellipsoidal zygospore is formed. The thin inner wall of each gametangium remains around the corresponding half of the zygote, the two membranes becoming fused together and forming a continuous wall. The investment so formed persists as the outer wall of the zygospore. Layers are subsequently deposited internally, resulting in a lamellated wall at maturity.

d. Spirogyra.

An examination of some twenty species of *Spirogyra* shows a remarkable similarity in the chemical composition of the vegetative cell walls and those of the zygospores, with the exception of the *Sirogonium* division of the genus, which will be described separately. In all species studied the filaments proper are surrounded with a mucilaginous sheath of pectose, varying considerably in thickness with the different species. In *S. flavescentis*, *S. Weberi*, and *S. catenaeformis* it is very thin and easily overlooked. With the species of larger diameter the amount of mucilaginous material is usually correspondingly increased. The thickest pectose sheath is found in *S. submaxima*, sometimes reaching a thickness of seventeen microns. Its permeability to reagents varies somewhat with age and water supply, but the exact factors of the environment responsible for such variation are still under investigation.

The cell wall beneath the pectose envelope is apparently in all cases composed of two layers, the innermost thin and delicate, covering the protoplasts; the outer is thicker and tougher; both are of cellulose. The replicate end walls of such species as *S. Weberi*, *S. protecta*, and *S. insignis* are merely annular ingrowths of cellulose which lead to fragmentation of the filament by becoming everted, as noted by West (41).

Stages antecedent to and accompanying conjugation have been noted in *S. majuscula*, collected in a roadside rivulet in July, 1922, and kept in aquaria. Outgrowths of cellulose occur usually about halfway between the ends of the conjugating cells. When these protuberances from adjacent filaments come into contact, the ends fuse, and disintegration of the planes of contact occurs soon after, resulting in a conjugation tube. Just what chemical changes occur in the absorption of the fused ends has not been followed in detail. It appears that the dissolved cellulose accompanies the male gamete into the female gametangium, entering into the formation of the

zygote. The conjugation tube is soon invested with a pectose covering and behaves as the rest of the filament toward color reactions and solubility tests.

In the formation of the zygospore after the fusion of the gametes, there is a further contraction of the fused protoplasts until they occupy a position about the center of the cells. At first only a thin transparent wall, surrounding the fused protoplasts, can be noted. Within one to three days the wall is seen to be composed of two layers, the outermost one considerably thicker than the inner. Upon the application of copperoxide-ammonia, the outer layer swells and occupies a volume from one and a half to six times its original size. As it goes into solution, (after fifteen minutes to one hour) the inner layer dissolves too, leaving a naked protoplast of contracted spirals. Within a week or ten days the spore is mature, and besides having another layer, it has taken on other properties. The outer layer and the inner layer are entirely of cellulose. The middle layer, very difficultly soluble in copperoxideammonia and isotropic in polarized light, often has deposits of chitin. In the rough-spored species examined, the spore markings were always associated with chitinous deposits. It is difficult to explain the irregularity deposited areas of chitin, for even in the smooth-spored species there is no continuous layer of chitin.

In the germination of the zygospore the outer walls are burst through by the developing sporeling. The inner membrane of the spore becomes the wall of the developing sporeling. In making microchemical analyses of the germinating spores one gets a definite test for chitin, but one must not incorrectly interpret this to mean that chitin is present in the young vegetative plant. Tests indicative of chitin were in every case the result of the reagent coming into contact with the middle layer of the old zygospore. Within a few days a pectose layer is noted around the sporeling, and repeated cell divisions result in the formation of a filament.

Separate mention should be made of *Spirogyra illinoiensis* and *S. stictica*, which belong to the Sirogonium (Choapsis) division of the genus. There is no real conjugation tube, but the walls of the gametangia come into contact, giving the filaments a genuflexed appearance similar to that described for *Mougeotia genuflexa*. A perforation is effected at the plane of contact by dissolving the cellulose and the contents of one

gametangium, after having completely disintegrated, pass over into the other. The fusion of the two results in a zygote.

Conjugation is not effected in all of the cells of the filament. Among certain cells there is noted a considerable decrease in size in direction of the length of the filament. The cell walls undergo slight thickening, and an increased amount of pectose is noted in the vicinity of the plane of contact of the two gametangia in apposition. Upon the complete coalescing of the two gametes in the female gametangium, a heavy somewhat differentiated wall is formed at the periphery of the fused protoplasts inside of, and not connected with, the wall of the gametangium. This wall is composed of three or more layers or coats. The outer one, anisotropic in polarized light, is usually pectose and can be completely removed after heating for one hour in 3% hydrochloric acid over a water bath and following this with warm 2% potassium hydroxide. The remaining layers of the wall are largely cellulose, but with considerable variation in solubility and reaction to polarized light. Upon the application of copperoxideammonia, an outer anisotropic layer dissolves in a few minutes. The remaining layer (sometimes layers) swells, is ruptured, and comes off the zygote like the covering of a much-used baseball. This shell is anisotropic in polarized light, is insoluble in cold concentrated sulphuric or hydrochloric acid, and fails to give the hydrocellulose reaction. If, however, the membrane remains in copperoxideammonia for from fifteen to twenty-four hours, it is completely dissolved. A further analysis of this membrane as it is dissolving shows that it has deposits of chitin, similar to that of the spores of the species of *Spirogyra* described above.

It is interesting to note that the gametangial walls behave almost exactly as the membranes of the zygospore. Upon the dissolving of the pectose membrane, the polarizer reveals a clear light layer surrounding a darker one. The outer is pure cellulose, but the inner has irregular deposits of chitin. The walls of the vegetative cells not concerned in zygospore formation are chemically identical with those of the other species of *Spirogyra* not belonging to the *Sirogonium* division.

In these two members of the genus two notable chemical differences occur. The zygospores have an outer layer of pectose and the fruiting cell becomes slightly shortened and the wall thickened and changed to the extent that the inner mem-

brane becomes chitinized. This together with their peculiar method of conjugation makes them an interesting division of the genus. West (41) has recommended that the generic name *Sirogonium* be retained for these forms. In view of the fact, however, that in many species like *S. tenuissima*, *S. punctiformis*, *S. circumlineata*, and others, the female furnishes little or no protuberance; that the gametangial walls of *S. ellipsospora*, *S. hydrodictya*, and *S. crassa* undergo changes in size and shape, as well as cell thickness, and that chitinous deposits in the gametangial walls are slight and sometimes wanting—it does not seem necessary or desirable to increase further the taxonomic nomenclature by providing another genus among the Zygnemaceæ for these variations.

Species of *Spirogyra* examined were the following: *Spirogyra varians*, *S. circumlineata*, *S. catenaeformis*, *S. flavescens*, *S. velata*, *S. daedalea*, *S. irregularis*, *S. ellipsospora*, *S. ellipsospora crassoidea*, *S. fluviatilis*, *S. novae-angliae*, *S. crassa*, *S. majuscula*, *S. hydrodictya*, *S. Weberi*, *S. laxa*, *S. tenuissima*, *S. tenuissima foveolata*, *S. inflata*, *S. protecta*, *S. rectangularis*, *S. insignis*, *S. stictica*, and *S. illinoiensis*.

3. *Microsporaceæ: Microspora.*

The filaments of *Microspora* are cylindrical and unbranched, and the character of the wall varies with different species. In *Microspora Willeana* the wall is distinctly lamellate, being constructed in such a way that upon disarticulation of the filament, H-pieces are formed. Each H-piece consists of two cup-like cylinders having a common base which forms the transverse wall of the filament. Each cylinder concavely thickened at its base becomes thinner toward the top. The fitting together of the H-pieces by the dove-tailing of these thinner parts forms the filament, so constructed that from an internal view a slightly concave H-piece alternates with one slightly convex, giving the whole filament a nearly cylindrical shape (Fig. 1). Thus each uninucleate cell is composed of two halves of supplemental H-pieces.

A microchemical analysis of *M. Willeana* shows that the reticulated chloroplast is surrounded by a thin wall of cellulose which, though appressed to the conjoined halves of two separate H-pieces, behaves as a unit. It can be noted after disarticulation of the filament, but it dissolves very quickly in copper-

oxidammonia. It gives a bright line with polarized light. The H-pieces themselves consist of more difficultly soluble cellulose, the overlapping pieces of which are connected by a very thin membrane that varies considerably in structure and nature. The whole is surrounded by a thin mucous coat of pectic acid and pectose.

The pectose layer on the outside sometimes extends inward for some distance between the appressed H-pieces, so that upon treatment with warm hydrochloric acid and dilute potassium hydroxide this inward protrusion is dissolved. As a result the filaments appear as in Fig. 2. There is a corresponding outward protrusion of the inner cellulose layer between the H-pieces (Fig. 2a). Continued immersion in copperoxide-ammonia for three to six hours causes the swelling of the inner cellulose wall with its outward protrusion, and the filament is ruptured, breaking up into H-pieces. And as if this were not sufficient complication, there is sometimes a small amount of calcium pectate connecting the outward extension of the cellulose and the inward protrusion of the outer pectose layer. There exists considerable variation in the amounts of these compounds. Often it is almost wholly cellulose, sometimes mostly pectose, and rarely of calcium pectate.

It is interesting to note that copperoxideammonia penetrates readily through the pectose and pectic acid layer, first swelling and finally dissolving the cellulose membrane. If the pectose and pectic acid be first removed, the whole filament appears bright under polarized light. Upon the application of cellulose-dissolving reagents, the remainder of the thin layer separating the dove-tailed H-pieces is dissolved, resulting in the disarticulation of the filament. The cellulose surrounding the protoplast then dissolves rapidly away—in fact almost as soon as the reagent strikes it. The H-pieces swell considerably, particularly at the transverse wall, and in from two to ten minutes are completely dissolved.

The formation of these peculiar H-pieces can be observed by watching the development of the plant during cell division. As soon as the cross wall is laid down, additional concave layers of cellulose are deposited internally at the juncture of the partition with the peripheral cell wall. A sporeling, having made its first cell division, as above, would consist of one H-piece the extremities of which are connected as in Fig. 3. The next

wall (or walls) formed similarly presents a formation like that shown in Fig. 4. Now upon the formation of a cross wall at *a* or *b* (Fig. 4), the concave thickenings are laid down, and as their extremities must necessarily underlap the extremities of the thickenings previously laid down, the latter H-piece is in reality within the cylinder formed by the halves of the older adjacent H-pieces. Upon the growth of the new H-piece the outer cylindrical shell is distended to breaking, the rupture usually occurring obliquely to the length of the filament. This new H-piece develops slightly concave inwards. Thus are formed a series of H-pieces, consisting of a piece slightly concave alternating with one slightly convex, seen from the inside of the filament. Further cell division in this region of the filament was not observed. Continual cell division at either extremity of the sporeling, as described above, accompanied by the deposition of concave thickenings of cellulose on either side of the new partition and consequent growth in length of the peripheral wall, forms a many-celled filament.

4. *Cylindrocapsaceæ: Cylindrocapsa.*

Another interesting genus of the Ulothrichales is *Cylindrocapsa*, of which *C. geminella* and the variety *minor* are quite common in Ohio. The filaments consist of ellipsoid cells frequently grouped in pairs and provided with a cell wall greatly lamellated. The whole filament is inclosed within a rather tough sheath of pectose and pectic acid, the latter being more abundant in the younger thalli. The lamellæ, however, are of cellulose and not pectic in nature. The cell wall proper is of cellulose more difficultly soluble than the apposed lamellæ, which strip off easily one after the other in cellulose-dissolving reagents.

5. *Tribonemaceæ: Tribonema.*

The filaments of *Tribonema* are apparently constructed much in the same way as are those of *Microspora Willeana*, previously described. Dovetailing is not so marked in *Tribonema*, and the cell walls are relatively thinner; but the characteristic H-pieces appear upon the disarticulation of the filament. A long H-piece usually alternates with a shorter one, the extremities of the latter being situated internally to those of the former. Bohlin (3) figures the cell wall as composed of

several apposed layers of pectic compounds. In polarized light the filament is usually dark and only rarely touched by the application of copperoxideammonia. The outer layer is uniformly of pectose and the others may be either pectic acid or pectose, very rarely cellulose. There is no indication of calcium pectate in the filament. It appears that the conjoined H-pieces are held together sometimes by pectic acid, but more often by pectose of a slightly greater solubility than the rest of the layers in warm dilute acids and alkalis.

Species examined were: *Tribonema bombycina*, *T. bombycina tenue*, *T. utriculosa*, and *T. minus*.

6. Cell wall formation in relation to algal epiphytes.

Algal species, epiphytic upon other algæ, are rather common among members of the Chlorophyceæ, as well as among the Myxophyceæ and Bacillariæ. The manner of epiphytism, while variable in form and degree, usually assumes one of four relations to the host plant: (a) gelatinous stalks, either simple or branched, of pectose secreted by the so-called stipitate diatoms; (b) holdfast cells (haptera) which arise as basal cells in the germinating spores of such algæ as *Oedogonium*, *Bulbochæte*, *Microspora*, *Chætophora*, and more rarely in some species of *Spirogyra* and *Zygnema*; (c) each cell of the alga either unicellular, filamentous, or thalloid in direct contact with the host, as in *Cocconeis*, *Chamæsiphon*, *Chætosphæridium*, and *Sykidion*; and (d) mere attachment to a plant or other substratum of such more or less macroscopic mucilaginous colonies as *Tetraspora* or *Apiocystis*. The mucilage here may be either pectic acid or pectose; and the two are sometimes present somewhat intermixed.

The pectose stalks of some of the diatoms are found usually only in the early spring. Sudden rises in temperature, which in some way hasten the conversion of pectose into water-soluble pectin, account for the pulses of diatoms in rivulets and streams, as the writer (34) has noted in another paper.

Oedogonium and *Bulbochæte* normally have cell walls in three layers, viz.: the outermost chitin, the middle one pectose, and the inner cellulose. The basal cell, however, is not uniform in this respect. That part of the holdfast wall directly in contact with the algal host has two layers, instead of three. Here the mucilaginous pectose, forming the middle layer of the cell

wall elsewhere on the filament, forms the outer layer and is directly appressed to the wall of the host. The inner layer is unchanged (Cf. Fig. 5).

In the dioecious nannandrous species of the Oedogoniales the male plants are epiphytic on the female plants. The androspores come to rest on the wall of the oogonium, the suffultory cell, or sometimes other cells and produce upon germination dwarf males, or nannandria. The basal cell of the dwarf males (or the whole nannandrium if it be unicellular) is attached to the female plant in precisely the same way as the holdfasts are attached to the host plant, as noted above (Cf. Fig. 6).

Hirn (15) in the drawings of his magnificent monograph of the Oedogoniales invariably shows that the outer layer of the wall of the basal cell does not extend all the way around the holdfast. He does not note, however, that the discontinuance of the outer cell wall layer is significant. This detail in his sketches is simply another evidence of the wonderful keenness of his observations.

The epiphytes can be detached from the host plant in all cases if the algæ are placed in pectose-dissolving reagents. The brownish-red salt of iron, as reported by Fritsch (11), deposited about the attachment surface of the basal cells of some algæ may or may not be present, and as far as my observations go contributes nothing directly to the attachment of the epiphytes.

Algal epiphytes are often found attached to species of Oedogonium, Bulbochæte, Cladophora, Pithophora, and Vaucheria at any time during their life cycle. These same epiphytes, if they occur at all, are not found on Spirogyra, Zygnema, or Mougeotia during their period of vegetative growth; that is, attachment to these algæ occurs normally only after the initiation of reproductive activities. The explanation is rather evident when one compares the cell wall composition of the two groups of host plants mentioned above. In the Oedogoniales the outer layer of the filament is usually chitin, while in the last three forms the outermost layer of the cell walls is pectose. The cell walls of the former group do not materially change with age, except in thickness by internal deposition of cellulose. In the species of Zygnemaceæ examined, on the other hand, there appears to be almost a continuous transformation of cell wall material during vegetative development.

There is considerable doubt among algologists as to the manner of formation of mucilaginous pectic compounds in the filamentous Conjugatæ. It has been pretty definitely shown by Klebs, Hauptfleisch, and Lutkemuller (according to West) that in the Desmids mucus is secreted through cylindrical pores which pass outward directly through the cell wall. West (41) inclines to the opinion that in many of the Chlorophyceæ, however, "much of the mucus arises by the conversion of the outer layers of cellulose into mucilaginous substances of varying degrees of solubility in water, and increments are constantly added by the gelatinization of successive layers."

Pores similar to those found in the Desmids are not visible in the cell walls of either Spirogyra, Mougeotia, or Zygnema. No pectose can be detected on the sporeling until after transverse wall formation has begun. As spore formation occurs in these algæ, the amount of pectose present becomes gradually decreased, until finally the cellulose layer is practically exposed. These observations, though somewhat indirect evidence, lend credence to the statement just quoted from West. At any rate, epiphytic algæ have not been observed upon the Zygnemacæ when the pectose layer is present.

The absence of epiphytic algæ from Spirogyra, Mougeotia, and Zygnema during their vegetative growth is explained by the fact that there is a gradual change of pectose into water-soluble pectin during this period. When the amount of pectose formed internally is equal to that dissolved externally, a sort of equilibrium is established, and the thickness of the pectose remains practically constant. When the activity is shifted in either direction, the pectose sheath is accordingly thin or thick. As spore formation begins, the formation of pectose stops. Pectin formation occurs until the pectose is exhausted, exposing the cellulose layer of the cell wall. Obviously, as long as the external pectose-to-pectin conversion takes place, epiphytic stability is decidedly uncertain. The cellulose, thus exposed, undergoes no further change until decay sets in, and epiphytes are found rather commonly at these stages.

III.

PROTOPLASMIC INCLUSIONS OF THE NATURE OF
FOOD RESERVES.

The principal food reserve in most of the green algæ during the period of their vegetative growth is starch. Exceptions to this general statement are the various species of *Vaucheria*, under normal conditions, and the *Heterokontæ*. In these latter algæ the food reserve is a fatty oil. Davis (9) in his historical resume of algological literature bearing directly or indirectly upon enzyme action notes the following: Beyerinck (2) found glycogen in *Chlorella variegata*. Kuster (19) reports crystal formation, probably inulin, in *Derbesia* and *Bryopsis*. Swartz (33) concludes that in *Enteromorpha* the carbohydrates exist as pentosans and galactans. Tihomirow (35), using the phenylhydrazine method, secured after a month yellow amorphous deposits in the cells of *Codium bursa* and *C. tomentosum* (both *Siphonales*). He could not determine the sugars these osazones represented, but suggested dextrose and *d*-galactose.

The algæ with which this phase of the work has been carried on include the species of *Zygnemaceæ* named in Part II above, and in addition *Cladophora glomerata*, *Pithophora varia*, *Vaucheria geminata*, *V. geminata racemosa*, and *V. hamata*.

Starches and Oils.—In the *Zygnemaceæ* and *Siphonocladiales* studied the starch is principally associated as an integral part of the pyrenoids. Under conditions of rather high photosynthetic activity it may be found outside the pyrenoids in the chloroplasts.

The amount of starch present has a daily as well as a seasonal periodicity. The former depends principally on the availability of sunshine. The latter is associated in some way with the changes in the metabolic gradient accompanying the different phases of the life cycle of the alga. The iodine test of an early morning before sunrise gives a definite reaction for starch only in the periphery of the pyrenoid. After an hour or more of sunshine, the whole chloroplast appears purplish. An examination of the spores of the algæ reveals the fact that in addition to the starch a considerable quantity of oil is present. The comparative percentages vary with the different spores, but the amount of starch present is slightly in excess of that of

the oil. Upon germination of the spore, the oil is used up, and no fats are discernible in the sporeling. During the vegetative growth of the plant, starch is predominantly the food reserve. As soon, however, as the reproductive period of the alga begins to be reached, the amount of oil present in the chloroplasts increases rapidly. The fully formed spore contains fats and starches, from 20% to 50% of which is estimated to be oils.

Carter (6) notes that in the autumn there is an accumulation of starch in the *Cladophoraceæ* in the form of small grains. The starch is lodged in the interstices of the protoplasmic reticulum of the chloroplasts. Many of the *Cladophoras* are perennial and carry on photosynthesis whenever there is an availability of sunlight and proper temperature.

The starch envelope has a rather intimate connection with the rest of the pyrenoid. In fact, the writer has not been able to get starch-free algæ in a living condition among the *Zygnemaceæ* or the *Siphonocladiales*. Algæ placed in the dark lose starch, as indicated by the lessened intensity of the iodine test. But even after decomposition and decay of the walls and protoplasts have begun, there can be still secured definite tests for starch in the cells.

West (41) has noted that the pyrenoids of the *Zygnemaceæ* are in the nature of aleurone grains. Treatment of the pyrenoids with a solution of nigrosin-picric acid brings out the protein crystals as yellowish-green and shows the surrounding globoids to be colorless. Around this, of course, appears the starchy envelope.

In species of *Vaucheria*, under normal conditions, the food reserve is a fatty oil, not starch. Pyrenoids do not exist in the genus *Vaucheria*, and it has been supposed by some that the oils may be the first synthetic products. *Dichotomosphon*, a genus closely related to *Vaucheria*, stores starch instead of oil. Evidence will be submitted later (See Part IV) to show that starch may under some conditions be the partial, if not the whole, food reserve, even in *Vaucheria*. The writer inclines strongly to the belief that the various food syntheses among the algæ are not different fundamentally from those of the higher plants. Although some evidence is at hand to substantiate this opinion, the proof does not yet seem sufficiently adequate to present at this time.

Sugars.—It has been a question of interest for some time as to what the first visible product of photosynthesis among the Chlorophyceæ really is. Microchemical and macrochemical tests for sugars in these algæ have been for the most part either negative or so indefinite that the actual sugars concerned are very uncertain. Some attempt has been made to ascertain what sugars, if any, are the first photosynthetic products. Tests were made in all cases upon material brought into the laboratory directly from ponds and streams nearby. This material, previously exposed to direct sunshine, had all evidence of carrying on photosynthesis at a rather high rate.

Upon the application of copper tartrate and 20% sodium hydroxide (Fluckiger's test) to algæ thus collected and washed in distilled water, crystals of cuprous oxide appeared in a short time after heating. The crystals were in the solution, however, and not within the cells. If this test indicates glucose, it appears that the sugar is in a very soluble state and diffuses through the algal walls very readily. Checking up this reaction with other sugar tests gave very indefinite results. Both Benedict's and Fehling's solutions gave copper crystals very tardily, indicating the presence of some reducing agent, but not necessarily glucose. The osazone tests were practically negative. Results similar to those reported by Tihomirow (35) noted above were obtained after periods of from three to five weeks. The sugars these osazones represent are not identifiable.

Sayre (32) working in this laboratory secures somewhat similar results on sugar tests in the guard cells of *Rumex patertia* leaves. He gets cuprous oxide crystals with Fluckiger's, Benedict's, and Fehling's solutions, but has been unable to get osazone formation.

If glucose be the first photosynthetic product in the algæ studied, it must be transformed very readily into starch. It seems that the ordinary sugar tests are not applicable. From the definiteness of the Fluckiger reaction it appears that one of the hexoses is present. The writer hopes to be able to secure some modifications of the ordinary sugar tests that will indicate the smallest quantity of sugars present and help clear up the primary carbohydrate syntheses in the green algæ.

Hemicelluloses.—In the algæ examined methyl pentosans appear to be absent. The mannose hydrazone reaction for mannan was negative. There are distinct color reactions

with the orcin- and phloroglucin-hydrochloric acid tests for galactan and araban, but localization was difficult. These pentosans appear to be a part of the protoplasts.

Tannins.—Tannins are mostly non-crystallizable colloidal substances and are rather generally distributed in plants. Haas and Hill (13) note the occurrence of tannins in *Spirogyra*, *Mougeotia*, and *Zygnema* in the cells in the form of numerous small vesicles. These authors review the work of Van Wiselingh, who concluded from his investigations that (a) tannins played an important role in cell wall formation in certain cases in *Spirogyra*; (b) cells about to conjugate are rich in tannins; (c) there occurs a gradual diminution of tannin as conjugation proceeds, until the zygospore at maturity contains a mere trace; and (d) upon the interruption of conjugation tannin accumulation continues until the death of the plant.

Tests with a number of species of *Zygnemaceæ* tend to confirm most of the results noted above, but give no supportive data for others. Tannins are notably absent from these algæ during the period of active vegetative growth. It is during this time that most wall formation occurs, particularly cross walls. In other words, as long as active cell division is occurring, tannin tests are negative. Just as soon, however, as active vegetative growth ceases and reproduction begins, there is an accumulation of tannins. The tannins are most abundant during the development of conjugation tubes and during gamete formation in the *Zygnemaceæ*. They rapidly diminish during the fusion of the gametes and are practically absent from the mature zygote. It appears that the tannins occur along with changes in the metabolic gradient accompanying the transition from a vegetative state to a reproductive state. That the tannins are used in the elaboration of other materials during spore formation seems certain, but further investigation is necessary to determine the exact use of these substances in the algæ.

Cladophora glomerata, *Pithophora varia*, and the species of *Vaucheria* examined gave negative results for tannins.

Tests for tannins are easily made with ferric chloride, osmic acid, or a solution of ammonium molybdate in concentrated ammonium chloride.

Inulin.—Tests for inulin gave negative results.

IV.

SOME MINERAL ELEMENTS.

Microchemical tests for minerals are difficult to make in the algæ with any degree of certainty of localization because the entire plant lives practically submerged in water. The presence of a mineral salt within the cell sap of an alga does not necessarily mean that it will enter into the metabolism of the cell. Toxic substances like copper sulphate which are fatal to *Spirogyra* even in extremely small concentrations are readily taken in through the cell walls. Attention has been directed principally to the mineral salts found in connection with the chloroplasts and the cell walls.

The following brief summary gives the results of investigations to date. More work is in progress, and the subject will be treated more completely at the conclusion of those investigations. Some particular work with certain algæ with artificial environment bears a direct relation to mineral content, and this is discussed under Part V below.

Iron.....Ferric compounds found in the chloroplasts.

Calcium.....In the form of calcium pectate in the middle lamella of the walls of some algæ. Calcium is necessary for colonial and filamentous integration even though a distinct calcium pectate layer could not be noted. The calcium pectate layer can sometimes be determined in the large *Oedogoniales* and in *Microspora Willeana*. Evidence will be submitted later to show that calcium is necessary in some way for the formation of the middle layer of pectose in some filamentous *Conjugatæ*.

Potassium.....In many *Spirogyras* yellowish crystals of potassium chloroplatinate are found upon the application of an aqueous solution of platinum chloride. These crystals are found with difficulty except when conjugation tubes are being formed. Potassium seems to be abundant at the place where new wall formation occurs accompanying conjugation.

Phosphorus.....Species of *Zygnemaceæ* immersed in a solution of ammonium molybdate in nitric acid shows ammonium-phospho-molybdate crystals in the protoplasts. The crystals are small and the yellowish center is not always evident. In about ten minutes, if washed in dilute hydrochloric acid and treated with a 1% solution of phenyl-hydrazine hydrochloride, a bluish color appears in the chloroplasts.

Magnesium.....Noted sparsely in the cell sap, but not in the chloroplasts.

V.

SOME ENVIRONMENTAL CHANGES AND THEIR EFFECTS ON
ALGAL GROWTH AND REPRODUCTION.

Continuous artificial illumination.—Recently Harvey (14) has attacked the problem of growing seed plants in artificial light. He found that a number of plants grew from seed to maturity and set good seed in continuous artificial illumination. Other plants bloomed but did not set seed. Potatoes produced good tubers.

The writer has had under investigation for some months various species of *Cladophora*, *Pithophora*, *Spirogyra*, *Zygnema*, *Cylindrocapsa*, and *Oedogonium*, exposed continuously to artificial illumination. In this experiment two two-hundred watt Mazda lamps were used over a water area of 4 square feet. The bulbs were two feet from the water with sufficient ventilation to prevent excessive heating. The apparatus consisted of a box two feet square and six feet long placed open end down in a tank of water in the greenhouse. Extending nearly to the top of the water from the bottom of the tank is a concrete post, through which an iron pipe carries water. Water escapes from the tank through the exit pipe. In this way water is kept in circulation, thus aiding in keeping the temperature within the box and without the box nearly constant. This gives excellent opportunity for the study of comparative growths of the same species of algæ in the same water under almost identical conditions, except sunlight is available in the one case, while in the other the algæ are exposed to continuous artificial illumination. The upper end of the box allows for the entrance of the electric connection and at the same time serves as an exit for the heated air.

The occurrence of holdfasts in many of the attached filamentous algæ is common. Transeau (37), Collins (7), West (41, 42), Borge (4), and others report holdfasts as occurring among certain forms of the *Zygnemaceæ*, which are usually unattached. Pierce and Randolph (28) found that the extensiveness of holdfast development in *Oedogonium* depended upon the roughness of the surface with which the zoospore came into contact before germinating. Fritsch (10) records that the rhizoidal ends of germinated zoospores of *Oedogonium capillare* develop much more slowly than the tip ends, the process requiring several hours.

My investigations with *Spirogyra*, *Zygnema*, and *Oedogonium* in continuous artificial illumination show that the rhizoids, when they occur, in these algæ are always negatively phototropic but not necessarily dependent upon a rough surface. Artificial illumination in some way causes rather excessive holdfast-like development in *Spirogyra majuscula*, *S. porticalis*, and *S. varians* from the ordinary vegetative cell. Bulges occur and develop from the middle of the cells which have every appearance of initial conjugation. The tubes develop very long and tortuous, sometimes branching, but never conjugate. The chloroplast pattern in these cells is much disarranged, sometimes is lost, and frequently no cross walls occur in the branch.

Pithophora varia in continuous artificial illumination exhibits some peculiarities of development that necessitate special mention. The first week of January, 1922, some healthy plants of this alga, found growing in the greenhouse under the diffuse sunlight of winter, were transferred to the constantly illuminated water. The initial stages of the formation of resting spores (sometimes incorrectly termed "akinetes") were observable in a few cells. Within a week after the transfer rapid movement of the main mass of cytoplasm and chloroplasts to the ends of the segments was noticed. The major movement was toward the swollen upper end of the segment. Starch and oil accumulation increased. A transverse wall formed separating the spore from the rest of the segment. If further movement of chloroplasts and cytoplasm continued after the completion of the first transverse wall, a second, a third, and even a fourth wall was laid down in rapid succession. Thus the spores occurred singly, in twos, in threes, or in fours. Very rarely a series of five resting spores are formed at the upper end of the segment. This process was completed within five days after the *Pithophora* was placed in artificial illumination. Mature spores in the tank from which the algæ were taken were not formed for two months afterward. The time required for the maturing of a spore is thus materially lessened by placing this alga in continuous artificial illumination.

It has been possible to follow the life cycle of this *Pithophora* still further under artificial light. After a dormant period of from four to six weeks the spores thus formed began to germinate. The old segments from which they were formed

were still alive, but showed no signs of rejuvenated activity. Under ordinary conditions of light the spores usually germinate in opposite directions from the two poles. A transverse wall early develops, the lower half giving rise to a more or less extensive holdfast, the upper half becoming the main part of the thallus. The spores under artificial illumination always germinate from opposite equatorial regions, at right angles to the direction from which the light comes. That is, there occurs a change in the polarity of the spore. One region germinates from two to five days sooner than the other. Neither region takes on the characteristics of a holdfast, and no transverse wall occurs in the spore. The two oppositely developing branches grow very long (sometimes three or four millimeters) before segmentation occurs.

Although initial germination is always at right angles to the direction from which the light strikes the spore, there is a subsequent turning of the upper end of the thallus toward the light. In a saturated atmosphere the upper ends sometimes extended above the surface of the water as much as a centimeter or two.

The segments produced from these spores began the formation of a second generation of spores in three weeks. The same movement of chloroplasts to the upper end of the segments, the formation of transverse walls, and the maturing of the spores were identical with the formation of the first spores. Under natural conditions spores are produced usually but once a year, and undergo a rather long period of dormancy. Under continuous artificial illumination the whole cycle from spore to spore was effected in three weeks.

The effects of artificial illumination upon so-called sexual conjugation have been observed in only one instance. *Spirogyra majuscula* in nature is a late spring or early summer annual, found in a fruiting condition usually from the last week in June to the middle of July. Some material of this alga, collected in early April of this year in a vegetative state, was placed in the artificially illuminated chamber at that time. Mature zygospores were observed on April 24, at least six weeks before the usual time out-of-doors. In the same tank, but not in the constantly illuminated box, the same alga four weeks after that date, showed no indications of conjugation.

From the two observations on *Pithophora varia* and *Spirogyra majuscula* noted above, one is led to conclude that the time

required to produce resting spores and zygotes in these two algæ was materially shortened. It must be stated, however, that the temperature of the water within the box is slightly higher than that outside. Just what effect this slightly higher temperature has, has not been ascertained.

The cell walls of *Cladophora*, *Pithophora*, *Cylindrocapsa*, and *Tribonema* are notably lamellated. It has been suggested that these lamellations may have some relation to the daily periodicity of sunlight. I have been unable to get any very conclusive data bearing one way or the other on this phenomenon. The lamellations in *Cladophora* are less in number and appear later under continuous artificial illumination, but are never absent. No appreciable differences were noted in the other algæ. The lamellæ are apparently a growth phenomenon not directly related to sunlight.

It was noted in a previous part of this paper that in *Vaucheria* the principal food reserve is oil. Species of *Vaucheria germinata* and *V. hamata* in continuous artificial illumination stored starch instead of oil. Sometimes there were both starch and oil present at the same time in the coenocyte. In those parts of the coenocyte developed after the plant was placed under artificial illumination starch was the predominant, sometimes entire, food reserve. These species of *Vaucheria* were grown both on moist soil and in water, and the results were practically identical as far as starch formation is concerned.

Some effects of calcium on colonial and filamentous integration. Some cultures of *Spirogyra*, *Cladophora*, *Cylindrocapsa*, *Tribonema*, and *Chlorella* in Knop's solution with or without calcium were kept in the greenhouse during the winter of 1922-23. Rayss (30) has observed that calcium salts in the proportion of .25 to 1.75% greatly favored coenobe production in *Coelastrum proboscideum*; lesser amounts tended toward coenobic disarticulation.

In cultures of Knop's solution without calcium the following observations were made. Checks with calcium in the solution showed practically normal growth.

Spirogyra.....Filaments either broke up into fragments or developed abnormally long cells. Cross wall formation inhibited. Middle lamella often partially formed.

Cladophora.....The plants grew practically normally.

Cylindrocapsa..The cells rounded and divided uniformly into four ellipsoid divisions, which never became zoospores. No cell division noted thereafter.

Tribonema.....Filaments extremely fragmentary, the isolated H-pieces being very common.

Chlorella.....The plant lost practically all semblance of a colonial aggregation.

I have noted elsewhere that microchemical tests for calcium in many of the green algæ gave negative results. The growth in these cultures contributes no proof as to the presence of calcium pectate in the algal cells, but in some cases it is shown that the absence of calcium in the surrounding media is responsible for colonial and filamentous disintegration. Apparently calcium is necessary for the formation of the middle lamella in these algæ. It remains to be determined whether this is a direct or an indirect effect on the formation of pectose.

Wall formation and permeability to copper sulphate.—It has been known for a number of years that most green algæ are rapidly killed by extremely dilute solutions of copper sulphate. Algæ quite resistant to the effects of this salt are *Cladophora* and *Pithophora*; less resistant are the *Oedogoniales*; and very susceptible are the *Zygnemaceæ*. Copper sulphate in the proportion of one part in a million parts of water is fatal to most *Zygnemaceæ*. It requires a concentration four times as great to kill *Cladophora* or *Pithophora*. Most *Oedogoniales* can withstand a concentration only twice as great.

A study of the nature of the cell walls of these algæ offers some explanation for their varying resistance or susceptibility to copper sulphate. The cell wall of the *Zygnemaceæ* is made up peripherally of a layer of pectose; most *Oedogoniales* have an outer layer of chitin; the cell walls of *Cladophora* and *Pithophora* are heavily chitinized on the outside. Young branches of the latter alga are much more readily killed than the older parts of the thallus. An examination of the cell walls of the younger parts shows, however, that chitinization has not been effected, or at least incompletely so.

It appears, then, that resistance to copper sulphate in the water is related to the amount of chitinization of the algal cell walls. Pectic compounds and cellulose are readily permeable to copper sulphate; chitin is much more difficultly permeable to the same copper salt.

SUMMARY STATEMENTS.

1. Among species of *Zygnemaceæ* studied the cell wall of the filament in the vegetative state is uniformly of cellulose, surrounded by a layer of pectose of varying thickness.
2. The outer layer of the vegetative cell of *Cladophora*, *Pithophora*, and species of the *Oedogoniales* is chitin.

3. The zygospores and aplanospores of the Zygnemaceæ have three or more cell wall layers: the inner cellulose, usually thinner than the others; the outer of cellulose, occasionally with peripheral pectose; and the middle of cellulose with irregular deposits of chitin. Ornamentations of the middle layer are associated with these chitinous deposits.

4. In *Spirogyra illinoiensis* and *S. stictica* the outer spore wall is pectose and the gametangial walls are similar in construction to those of the zygotes.

5. The layers constituting the thickened gametangial wall in *Debarya decussata* are of cellulose, not of pectose.

6. The middle lamella of the cross walls of *Spirogyra*, *Mougeotia*, and *Zygnema* is uniformly of pectose, completely enveloped by cellulose.

7. Fragmentation of a filament in the Zygnemaceæ is brought about by the transformation of the pectose of the middle lamella into water-soluble pectin.

8. The cellulose H-pieces of *Microspora Willeana* are joined at their extremities by pectose or occasionally by calcium pectate. An inner layer of cellulose, independent of the H-pieces, surrounds the reticulated chloroplasts. The amount of pectose material present in the cell walls decreases with the age of the filament.

9. The lamellations of the cell walls of *Cylindrocapsa* are of cellulose. The whole is surrounded by a pectose sheath.

10. The cell walls of *Tribonema* have correspondingly lessened amounts of pectic compounds with increased age. The cell wall construction is very similar to that of *Microspora Willeana* described above.

11. Epiphytic algæ are usually attached to the host plant by a gelatinous layer of pectose.

12. In the Oedogoniales the outer chitinous layer is not present in those parts of the holdfasts and nannandria attached to the host, thus making the pectose layer peripheral at the points of attachment.

13. Epiphytic algæ do not usually occur on vegetative filaments of the Zygnemaceæ until there is a cessation of the transformation of pectose into water soluble pectin. This transformation usually ceases with initiation of reproductive activities.

14. Starches and oils are the principal food reserves of the green algæ studied.

15. Tests for sugars were not conclusive, although there is some evidence of the presence of glucose at the periods of greatest photosynthetic activity.

16. Color reactions for the pentosans, araban and galactan, were positive. No evidence of other hemicelluloses was secured.

17. Inulin tests were negative.

18. Tannins were not found in the green algæ during the vegetative period. Upon the initiation of reproduction the amount of tannin increases rapidly. The amount decreases during spore formation and there is scarcely a trace of tannin in the mature zygote.

19. Iron is present as ferric compounds in the chloroplasts.

20. Potassium is noted chiefly in the Zygnemaceæ at the time of conjugation in the region of the appressed areas of the conjugation tubes.

21. Calcium was observed in the larger Oedogoniales and occasionally in Tribonema. This mineral appears to bear some relation to the formation of the pectose middle lamella in the Zygnemaceæ, but tests for calcium in these algæ were negative.

22. Continuous artificial illumination reduces the life cycle period of *Pithophora varia* to three weeks; changes the polarity of the germinating resting spores ("akinetes"); and inhibits rhizoidal formation in this alga.

23. Constant artificial illumination causes the formation of mature zygotes in *Spirogyra majuscula* from six weeks to two months earlier than out-of-doors.

24. Lamellations in cell walls, whether of cellulose or of pectose, are not materially altered by constant artificial illumination.

25. The food reserve of species of *Vaucheria* under constant artificial illumination may be partially or wholly starch.

26. The absence of calcium from Knop's solution used as a culture medium produced colonial and filamentous disintegration in the algæ studied.

27. Calcium seems to have some necessary effect upon the initiation of cross walls in the septate filamentous algæ.

The writer is greatly indebted for suggestions and criticisms during the course of these investigations to Professors H. C. Sampson and E. N. Transeau, of the Department of Botany, Ohio State University.

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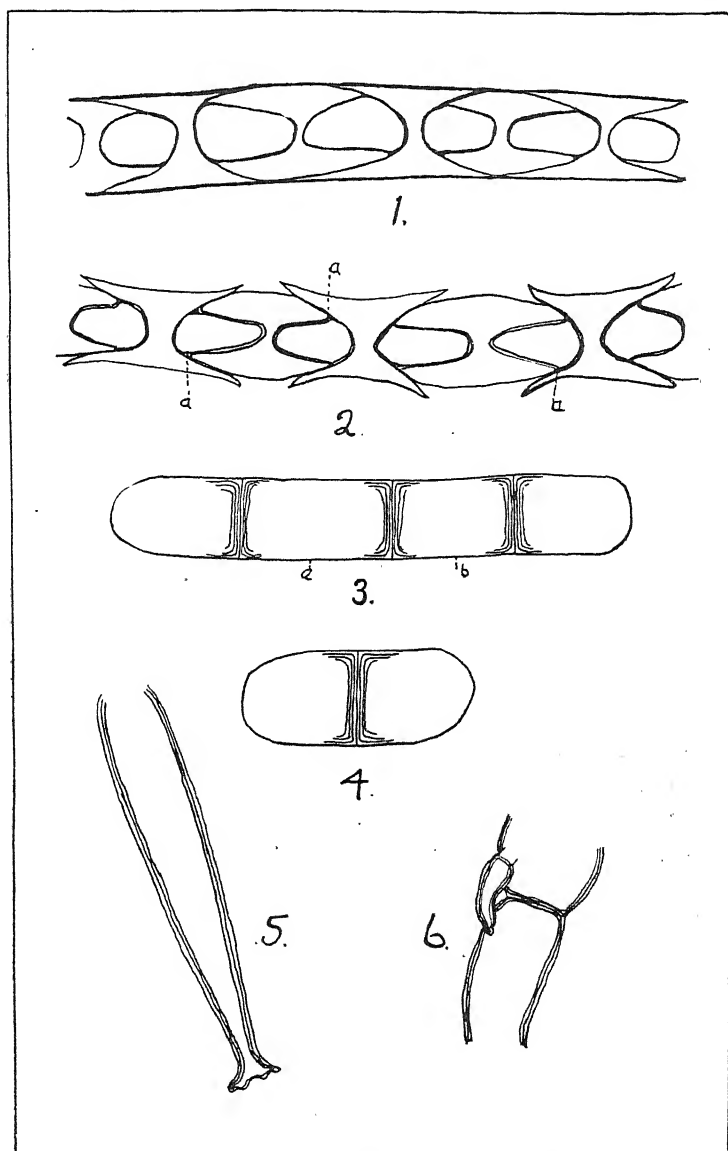


Fig. 1. Filament of *Microspora Willeana* Lagerh. under normal conditions.

Fig. 2. Same after treatment with warm HCl and KOH.

Fig. 3. Sporeling of *Microspora Willeana* Lagerh. with first transverse wall and pectose thickenings.

Fig. 4. Further transverse divisions of sporeling, indicating (a and b) where next cross walls will be laid down.

Fig. 5. Basal cell of *Oedogonium exocostatum* Tiffany showing dual nature of cell wall at points of attachment; triple nature elsewhere.

Fig. 6. Nannandrium on suffultory cell of *Oedogonium concatenatum* (Hass.) Wittr. showing dual nature of cell wall at points of attachment; triple nature elsewhere.

(All somewhat diagrammatic; see text for further explanation).

INSECT FOOD HABITS AND VEGETATION.

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INTRODUCTION.

The object of this paper is to call attention to the types of insect food habits which appear to be associated with certain types of vegetation. For the past three years, what might be called "insect surveys" have been made in different parts of New Jersey, primarily for the purpose of arriving at the relative importance of the food-habit types in various localities. In all cases an effort was made to obtain a fair sample of the species present and in order to achieve this end, all collecting methods were employed and the areas under consideration were visited, usually, at weekly intervals throughout the insect seasons. Whereas such methods are not exhaustive it is believed that a fair "sample" was obtained during each survey. The collections were all made by the same men, the same methods were employed throughout and the areas were collected over with the same degree of thoroughness, thereby making the results more comparable than if different methods and collectors had been employed in each case.

The types of food habits were based mainly on the predominating larval habits of the family and the results therefore are general, due to the absence of exact knowledge for many of the species concerned. Any classification of this sort will of necessity lack exactness, but the present state of our knowledge will not permit any better or quicker method. Under this plan each species was placed in accordance with its food habits, if known, and in accordance with its family food habits if its own habits were not known. Dr. L. O. Howard, in his paper on "The Economic Status of Insects as a Class," (Smith. Rept. 1898, pp. 551-569), published some twenty years ago, called attention to the difficulty of classifying insects in accordance with their injurious or beneficial habits, other than by summarizing their activities by families and the same difficulty will persist until the habits of many individual species are better known. In addition, the percentages showing the comparative

importance of the various types of food habits were founded on the species present, regardless of the number of individuals of each species. In some ways this might be regarded as a serious error. On the other hand, the fact that various species of insects exist indicates that they are adapted to their surroundings, including natural enemies, weather, diseases, etc., and if a species is plentiful or rare, such conditions are usually normal. Various species maintain themselves in certain numerical ratios with respect to factors or combinations of factors tending to reduce their numbers and also bear certain relationships to associations of plants. These relationships are usually normal and are part of the so-called natural balance except where the balance has been overthrown by the destruction of natural plant associations and the interposition of large numbers of plants belonging to a single species, or except where it has been temporarily destroyed by an unusual increase in the numbers of certain species of insects.

As natural conditions prevailed in the surveyed places, the numerical ratios can be considered as constant and the percentages showing the importance of the various types of food habits can be taken as indicative of conditions in the surveyed areas or other areas where plant associations, temperature, moisture, etc., are similar. It is not supposed that the percentages will be taken literally. They simply show the trend and the comparative importance of the food habit types in a general way. They should be considered as averages. As is well known, the accuracy of any average depends in part on the number of items on which the average is founded. The larger the number of items, the more accurate becomes the average. The absence of bias also increases the accuracy of the average. Absolute accuracy is not possible of attainment in a matter of this kind. It is realized that a much better picture of the relationships of the food habit types could have been drawn had figures on the numerical abundance of the species been available. Having such figures some weight could be assigned to each species and its importance in the general scheme of things partly arrived at. On the other hand, even though such figures were available, the fact that a certain species was present in large numbers would not be a true index as to its importance. Relative damage to plants and its relation to other insects would have to be considered. It

would be exceedingly difficult to assign to any one species the exact importance which it bears to the whole community of plants and insects.

It has been suggested that actual counts of the numbers of the various species should have been made in different parts of the surveyed areas and such figures applied to the entire areas. The physical difficulties of such a plan are obvious. Collecting varies from day to day and even from hour to hour and insects are not equally distributed among the plants of any area. Moreover the opportunity for errors would be very great if such a plan were followed. The assumption that the numerical ratios are constant within certain limits, where natural conditions prevail, simplifies the matter considerably. By natural conditions, it is meant that the vegetation was relatively unchanged by the hand of man. An outbreak of a certain species under such natural conditions would not in most cases affect the percentages given, in view of the fact that each species, regardless of its abundance or damage, is given the same weight. It is conceivable, of course, that a certain species might multiply to such an extent as to seriously injure its host and thereby start a train of events some of which might seriously affect many other species, thereby changing the ratio of the food habit types, but even if this happened, nature would restore the balance in due time. Moreover, numerical abundance varies from time to time and depends upon variable factors and figures or estimates secured during one season might not be applicable another season. Prof. Charles T. Brues, in his recent article on "Choice of Food and Numerical Abundance Among Insects," (*Jour. Econ. Ent.*, vol. 16, pp. 46-51), states that "the numerical abundance of a great many species of insects, perhaps of nearly all, depends to a very limited extent upon their powers of reproduction and almost entirely upon the factors which tend to limit these powers. Among these, the prevalence of disease, of insect parasites and the extent of the available food supply are the factors that determine how far any species may utilize its latent powers for reproduction and multiplication. All three factors are highly variable and to one or the several in combination may usually be traced the numerical abundance of any particular species."

THE SURVEYED AREAS.

At Monmouth Junction, N. J., the surveyed area was made up of about fifteen acres of moist woods on the Piedmont Plain of New Jersey. The ground was moist with many wet spots, but seldom became swampy. Among the trees, the red maple was the dominant species. This together with the oaks (*Q. palustris*, *rubra*, *alba*) contributed over half the trees in the woods, the balance consisting of ironwood, sweet gum and beech, with scattering clumps of gray birch in various stages of decay. A rich fungous flora, consisting mainly of polypores, flourished on the many trees and stumps in various stages of decay and the moist forest floor supported numerous species of gill fungi. Adjoining the woods was the thicket, about seven acres of which were included in the survey. In this area the fungous flora was negligible. Many of the characteristic plants of the tree and shrub groups in the woods held important places in the thicket and in addition, the herbaceous flora was large and complicated. It began with a spring flora, was followed by a less well-defined early and late summer series and ended with a distinct and showy autumn group.

The surveyed area at Lakehurst, N. J., was located in the "pine barrens" and consisted of about ten acres of dry woods and about four acres of adjoining open territory. The trees in the woods were almost entirely oaks and pines, with about two-thirds of the individuals pitch pine (*Pinus rigida*). The other third was made up of post oak, black-jack oak and chestnut oak, with a sprinkling of yellow pine and sassafras. The dominant shrub in the woods was the scrub oak. Others were clumps of scrub chestnut-oak, young pines and oaks, dangleberry and low blueberry. Herbaceous plants were few in number and inconspicuous. The open area was devoid of trees and contained such plants as the beach plum, blueberry, bearberry, patches of sweet fern, occasional plants of bayberry, large patches of dwarf sumac and many bare, sandy spots. Among the herbaceous plants were pine barren heather, sandwort, ipecac, toadflax, prickly pear cactus, horse-mint, etc.

The surveyed area at Morgan, N. J., consisted of about five acres of salt marsh located on the upper New Jersey coast along the Cheesequake creek and covered mostly by *Spartina*

patens and *Juncus gerardi*. This marsh was above mean high tide, but was occasionally covered by spring and fall tides and by winter and storm tides.

TYPES OF FOOD HABITS.

The following table (I) shows the types of food habits present in the various areas and their relative importance, the percentages being based on the species present regardless of numerical abundance.

TABLE I.

	Species	Phytophagous %	Saprophagous % *	Har- pacto- phagous %	Para- sitic %	Pollen Feed- ers %	Misc. %
Moist woods on Piedmont plain. Monmouth Jc.....	415	37	35	20	5	3	
Thicket, Piedmont plain. Monmouth Jc.	273	63	9	19	7	2	
Dry woods in "pine barrens" Lakehurst	381	45	21	18	14	2	
Open area in "pine barrens" Lakehurst	246	41	10	24	18	7	
Salt marsh, Morgan..	210	39	21	26	13	1	

TABLE II.

Western Arctic Coast of N. A.....	400	47	27	14	10	2	
State of N. J.....	10,500	49	19	16	12	2	2

According to Table I, the percentages of phytophagous and saprophagous species in the moist woods were almost similar and this is in accordance with what one would expect, knowing the conditions which included the presence of much decaying vegetation. The adjoining thicket on the other hand showed a small percentage of saprophagous species and a very

* J. Percy Baumberger, on the basis of experiments and "the general lack of nutritive value (for insects) of many" substrata assumes that the food of insects permanently inhabiting "substrata of a fermenting or delaying nature is the micro-organisms" (fungi and bacteria) found in such places, "and to a less extent the substratum." In view of this interpretation of the food of scavengers, he suggests that all insects which have in the past been termed scavengers, coprophages, etc., be included under the term Mycetophages. (Jour. Exp. Zool. Vol. 28, 1919, pp. 1-81.)

large percentage of phytophagous ones. This, too, appears to be natural in view of the absence of conditions which would support saprophagous species and because of the presence of a large herbaceous flora, plenty of sunlight and higher temperatures, all of which would account for the larger percentage of phytophagous species. In both the thicket and woods, the remaining percentages are approximately similar showing that the other types of food habits were about of equal importance with respect to the species present. This, too, might be expected in view of the fact that both areas were adjoining and generally similar although differing in details.

Almost the same thing holds true of the "pine barren" woods and its adjoining open area. The percentages of phytophagous forms were almost similar in each. The woods with some dead timber and decaying vegetation showed more saprophagous species than the open area. The predaceous and parasitic species were also about equal in each, the actual difference shown in the table not being large enough to be of any significance.

Comparing the moist woods, dry woods and salt marsh with each other, it is found that the percentages of phytophagous species do not vary greatly and that only in the moist woods is there a decided increase in saprophagous species. The percentages dealing with predaceous food habits show comparatively little variation, being highest for the salt marsh and lowest for the dry woods. Scanning the "parasitic" percentages, it is found that the lowest figure is for the moist woods and the highest for the dry woods, if the thicket and open area are left out of consideration. These figures do not appear to be as consistent as the others and it is not known why comparatively fewer parasitic species should occur in the moist woods area, although a small percentage is not inconsistent with a "balance" when nothing is known of the numerical abundance of the species.

As a matter of interest the food habits of the 10,500 species of insects recorded from New Jersey and the some 400 species reported from different sections along the Western Arctic Coast of America, (Rept. Canad. Arc. Exped., vol. III, Insects, parts A to K), have been tabulated and these percentages which are shown in table II are strikingly similar and seem to indicate that the ratios between the various types of food

habits are approximately identical or vary but little when large areas embracing different types of vegetation are considered *in toto* and when the numerical ratios between the species and the factors tending to reduce their numbers are considered as constant, or at the most fluctuating within limits which do not allow any serious disturbance of the "natural balance."

The percentages shown in table I for different portions of New Jersey appear to indicate that the ratios between the various types of insect food habits, (based on the species present, with the numerical ratios between the species and the factors tending to reduce their numbers considered as approximately constant) vary in accordance with the type of vegetation when relatively small areas each with a uniform type of vegetation are considered.

ADDITIONS TO THE CATALOG OF OHIO VASCULAR PLANTS FOR 1923.*

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The past year has been one of unusual activity in the study of the Ohio flora and many important additions have been made to the State Herbarium. A. D. Selby, of the Ohio Experiment Station at Wooster, presented a fine collection of willows—91 sheets of specimens from other states and 67 sheets of Ohio species. Those which extend our knowledge of the distribution in the state are listed below. Charles C. Deam, state forester of Indiana, looked over the species of *Vitis*. A. R. Harper and Edw. S. Thomas, of Columbus; Katie M. Roads, of Hillsboro; E. Lucy Braun, of Cincinnati, and others have made important contributions.

All the specimens of the genus *Carex* were studied by Kenneth K. Mackenzie, the sedge specialist. The determinations of the species of this difficult genus are, therefore, as accurate as it is possible to make them. A complete revision of the *Carex* list is given below with the distribution as indicated by the herbarium specimens. The numbers correspond to the original list as given in the Catalog and are in the correct phyletic sequence. This list will now be a new starting point for the study of Ohio sedges. There are, no doubt, many species not yet listed, especially in the bogs and swamps of the north-eastern part of the state.

11. Change name to *Polypodium virginianum* L. Virginia Polypody. According to the studies of M. L. Fernald, our species in the eastern United States is distinct from the European *P. vulgare* L. and was so recognized by Linnaeus.
58. *Lycopodium lucidulum* Mx. Shining Clubmoss. In Cedar Swamp, near Urbana, Champaign Co. Robert B. Gordon.
68. *Pinus strobus* L. White Pine. Pine creek and Mohican river, Hanover Twp., Ashland Co. "Probably extends into Worthington Twp., Richland Co." Mrs. Bayard Taylor.

*Papers from the Department of Botany, The Ohio State University, No. 146.

71. *Pinus echinata* Mill. Short-leaf yellow Pine. "Collected west of Sugar Grove, in pine tract. Several trees noted." Fairfield Co. G. G. Hedgcock. The writer has looked for this species at Sugar Grove several times in the past, but evidently missed the right place.
76. *Taxus canadensis* Marsh. American Yew. Paint Twp., Highland Co. August E. Miller.
80. *Sagittaria rigida* Pursh. Sessile-fruited Arrow-head. East of Newark, Licking Co. Robert B. Gordon.
134. *Wolffia punctata* Griseb. Punctate Wolffia. In pond. Jackson Twp., Franklin Co. John H. Schaffner.

REVISED LIST OF THE SPECIES OF CAREX.

- 182, 183. Stet.
184. Fairfield, Ottawa, and Wayne counties.
185. General, but no specimens from the southwestern part of the state.
- 185.1. *Carex convoluta* Mackenzie. General.
- 185.2. *Carex radiata* (Wahl.) Dew. Radiate Sedge. Erie, Geauga.
- 186, 188, 189, 191, 193. Stet.
187. Lucas, Erie, Summit.
- 187.1. *Carex plana* Mackenzie. Reported by Mackenzie in November, 1923, Bull. Torr. Bot. Club. Specimens in Gray Herbarium, Harvard University. Collected by Moseley on Catawba Island, Ottawa Co.
- 188.1. *Carex leavenworthii* Dew. Leavenworth's Sedge. Ottawa, Hardin.
190. Cuyahoga Co. only.
- 191.1. *Carex aggregata* Mackenzie. Glomerate Sedge. Licking Co.
192. Rather general, but no specimens from eastern or southern counties.
- 193.1. *Carex annectens* Bickn. Yellow-fruited Sedge. Cuyahoga, Erie.
- 193.2. *Carex brachyglossa* Mackenzie. Reported by Mackenzie in November, 1923, Bull. Torr. Bot. Club. Specimens in Gray Herbarium, Harvard University. Collected by Moseley, Oxford, Erie Co.
194. No specimens. The specimen so named is *C. annectans* Bickn.
195. Lake, Summit.
196. Erie Co.
- 197, 201, 202. Stet.
198. From Tuscarawas, Franklin and Champaign Cos. northward.
- 198.1. *Carex laevi-vaginata* (Kuekenh.). Mack. Butler, Franklin, Delaware, Madison, Hocking, Licking, Stark.

- 199. Defiance, Auglaize.
- 200. No specimens.
- 203. Logan, Lake.
- 204. No specimens. The specimen so named is *Carex bromoides* Schk.
- 205. Lake, Cuyahoga, Erie, Hancock, Hardin, Auglaize.
- 206. Erie County.
- 206.1. *Carex sterilis* Willd. Erie, Madison.
- 206.2. *Carex howei* Mackenzie. Howe's Sedge. Stark, Wayne, Summit, Perry, Licking.
- 207. Change name to *Carex cephalantha* (Bail.) Bickn. Little Prickly Sedge. Portage, Lake.
- 207.1. *Carex incompta* Bickn. Prickly Bog Sedge. Geauga County.
- 207.2. *Carex seorsa* E. C. Howe. Cuyahoga Co.
- 208. Northern Ohio, as far south as Carroll. Tuscarawas, Knox, and Williams Counties.
- 209, 210, 211. Stet.
- 212. Lorain county only.
- 213. Change name to *Carex tenera* Dew. Lake, Lucas, Williams.
- 213a. Unpublished varietal name. Will be supplied later.
- 214. General, but no specimens from the southeastern counties.
- 214.1. *Carex brevior* (Dew.) Mack. Lake, Logan, Erie, Madison, Hamilton.
- 215. Tuscarawas, Cuyahoga.
- 215.1. Unpublished species. Will be supplied later.
- 216, 219, 220, 222, 223, 225. Stet.
- 216.1. *Carex merritt-fernaldi* Mackenzie. Lake county.
- 216.2. *Carex suberecta* (Olney) Britt. Prairie Straw Sedge: Auglaize, Champaign.
- 217. Stark, Summit, Cuyahoga.
- 218. Omit from the list.
- 221. General, but no specimens from the south-eastern counties.
- 224. General in distribution.
- 226. From Erie, Madison, and Hamilton Counties eastward.
- 227. From Lake, Tuscarawas, Franklin, and Warren Counties northwestward.
- 228, 229, 230. Stet.
- 231. No specimens.
- 232. No specimens.
- 233. Lake and Erie Counties.
- 233.1 *Carex woodii* Dew. (*C. colorata* Mackenzie) Wood's Sedge. Huron, Auglaize, Erie, Cuyahoga, Geauga.

234. Cuyahoga, Summit, Lorain, Huron, Fairfield, Clarke.
235. Lorain, Franklin, Vinton.
236. From Cuyahoga, Delaware, and Hocking counties eastward.
237. Lake, Cuyahoga, Erie, Lawrence.
238, 239, 242. Stet.
240. General in distribution.
241. Change name to *Carex gracilescens* Steud. Rather general.
242.1. *Carex striatula* Mx. Striate Sedge. Lawrence county.
243. Lake and Defiance counties.
244, 245, 248. Stet.
246. Hamilton, Montgomery, Green, Ross, Franklin, Licking, Tuscarawas.
247. Hamilton, Butler, Highland, Auglaize, Lake.
249. No specimens; all so reported are *C. grisea* Wahl.
250, 253, 255, 256. Stet.
251. Williams, Cuyahoga.
252. Northern Ohio, as far south as Hocking County.
254. *Carex davisii* Schw. & Torr. Davis' Sedge. Lake, Lorain, Auglaize, Licking, Ross, Hamilton.
256.1. *Carex swanii* (Fern.) Mack. Northern Ohio, as far south as Auglaize, Madison, and Summit counties.
257. Lake, Cuyahoga, Knox, Licking, Fairfield, Hocking, Lawrence.
258. Change name to *Carex hirsutella* Mackenzie. Hirsute Sedge. General.
258.1. *Carex caroliniana* Schw. Carolina Sedge. Tuscarawas County.
259, 262, 263, 265. Stet.
260. Licking and Ashtabula counties.
261. No specimens. The specimen so reported is *C. limosa* L.
264. Change name to *Carex strictior* Dew. Tussock Sedge. Champaign, Madison, Marion, Lake, Erie, Lucas, Defiance, Auglaize.
266. Cuyahoga, Erie, Knox, Franklin, Hocking.
267. Change name to *Carex aquatilis substricta* Kuekenh. Water Sedge. Auglaize, Lucas.
267.1. *Carex emoryi* Dew. Emory's Sedge. Lake, Cuyahoga, Trumbull, Hardin, Delaware, Hamilton.
268. Harrison county.
269, 272, 273, 274, 275. Stet.
270. Lake, Cuyahoga, Summit.
271. Erie, Morrow, Logan, Hardin, Seneca, Hancock, Lucas, Auglaize, Defiance.
276. Change name to *Carex irregularis* Schw. Erie County.
277. No specimens.

- 277.1. *Carex cryptolepis* Mackenzie. Lake County.
278. Portage County.
279. No specimens.
280. *Carex vesicaria* L. Inflated Sedge. Lake, Cuyahoga, Wayne, Lucas.
281. Lake, Geauga, Licking.
282, 283, 284, 285, 286. Stet.
287. No specimens. All so reported are other species.
288, 290, 291, 292, 293. Stet.
289. General in distribution.
293.1. *Carex macounii* Dew. Macoun's Sedge. Lorain County.
294. General in distribution.
295. Warren, Marion, Crawford, Wayne.
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- 321.1. *Uniola latifolia* Mx. Broadleaf Spike-grass. "On ledge along Little Scioto River." Scioto County. A. R. Harper.
384. *Sporobolus vaginæflorus* (Torr.) Wood. Sheathed Rush-grass. "On dry hills." Washington Twp., Highland County. Katie M. Roads.
410. *Aristida dichotoma* Mx. Poverty-grass. "Common in sterile field." Washington Twp., Highland County. Katie M. Roads.
412. *Aristida gracilis* Ell. Slender Triple-awned-grass. Mt. Oreb, Brown County. Unusually tall form in "disturbed ground, 'white clay.'" E. Lucy Braun.
465. *Holcus halapense* L. Johnson-grass. Fairfield County. A. R. Harper.
466. *Holcus sorghum* L. A variety of Broomcorn. In waste lot. Hillsboro, Highland County. "A common volunteer in Liberty and Penn Twps., Highland County." Katie M. Roads.
468. *Miscanthus sinensis* Anderss. Chinese Plume-grass. In vacant lot near Hillsboro, Highland County. Katie M. Roads.
469.1. *Andropogon elliottii* Chapm. Elliott's Beard-grass. "Common in the pine forest on hills, mixed with *Andropogon scoparius* Mx." Sugar Grove, Fairfield County. E. N. Transeau.
470. *Andropogon virginicus* L. Virginia Beard-grass. A single plant along road south of Canal Winchester, Madison Twp., Franklin County. Abundant on hills, especially in pastures and old orchards in Bloom Twp., Fairfield County. John H. Schaffner. Also Hillsboro, Highland County. Katie M. Roads.
499. *Chamælirium luteum* (L.) Gr. Chamælirium. Old Man's Cave, near South Bloomingville, Hocking County. Mrs. Bayard Taylor.

504. *Trillium declinatum* (Gr.) Gleason. Drooping Trillium. Delaware County. Robert B. Gordon.
539. *Juncus bufonis* L. Toad Rush. Eastwood, Brown County. "Cleared land," on "white clay." E. Lucy Braun.
549. *Juncus canadensis* J. Gay. Canada Rush. In swamp near Hillsboro, Highland County. Katie M. Roads.
555. *Manfreda virginica* (L.) Salisb. False Aloe. "Found general on limestone ledges with shallow soil." Adams County. A. R. Harper.
559. *Gemmingia chinensis* (L.) Ktz. Blackberry-lily. At base of limestone cliffs near Blue Creek Post Office, Adams County. A. R. Harper.
560. *Crocus vernus* L. Spring Crocus. "Escaped to waste places. Hillsboro, Highland County. Katie M. Roads.
580. *Blephariglottis peramoena* (Gr.) Rydb. Fringeless Purple Orchis. "Collected by Mr. and Mrs. Percy C. Roads in a damp woods." Union Twp., Highland County. Katie M. Roads.
583. *Triphora trianthophora* (Sw.) Rydb. Nodding Triphora. Sugar Grove, Fairfield County. Robert B. Gordon.
600. *Corallorrhiza maculata* Raf. Large Coral-root. "In thicket along road, near Blue Creek P. O.," Adams County. Arthur R. Harper.
- 619.1. *Ranunculus pucillus* Poir. Dwarf Crowfoot. Goshen Station, Clermont County. "In shallow pools." E. Lucy Braun.
696. *Radicula sylvestris* (L.) Druce. Creeping Yellow-cress. "On the bank of a small stream." A rare plant along most of our small streams." Hillsboro, Highland County. Katie M. Roads.
712. *Norta altissima* (L.) Britt. Tall Hedge-mustard. In waste ground. Columbus, Franklin County. John H. Schaffner.
755. *Cleome spinosa* L. Spider-flower. A considerable patch developed in a waste place. Columbus, Franklin Co. John H. Schaffner.
- 760.1. *Geranium dissectum* L. Cut-leaf, Crane's-bill. University of Cincinnati Campus, Cincinnati, Hamilton County. "Weed in fill." E. Lucy Braun.
- 774.1. *Linum striatum* Walt. Ridged Flax. Kluck's Crossing, Clinton County. "Meadow, 'white clay' area." E. Lucy Braun.
- 785.1. *Polygala incarnata* L. Pink Milkwort. Buena Vista, Scioto County. Arthur R. Harper.
816. *Callitriche heterophylla* Pursh. Goshen Station, Clermont County. "Shallow ponds." E. Lucy Braun.
- 828.1. *Hibiscus syriaca* L. Shrubby Hibiscus. Propagates itself readily from seed in Columbus, Franklin County. John H. Schaffner.

854. *Lechea minor* L. Thyme-leaf Pinweed. Butler Springs, Highland County. "Dry south slopes, oak-sumach." E. Lucy Braun.
966. *Salsola pestifer* Nels. Russian-thistle. Quite frequent in waste places. Columbus, Franklin Co. John H. Schaffner.
992. *Persicaria orientalis* (L.) Spach. Prince's-feather. "Occasional in waste places and pastures." Hillsboro, Highland County. Katie M. Roads.
1024. *Rubus hispidus* L. Hispid Dewberry. Kluck's Crossing, Clinton County. "Pin oak woods, openings." E. Lucy Braun.
1097. *Cassia medsgeri* Shaf. Medsger's Senna. Near Mt. Oreb, Brown County. "In shrub meadow, depression in 'white clay.'" E. Lucy Braun.
1112. *Trifolium agrarium* L. Yellow Hop Clover. Near Newark, Licking County. Robert B. Gordon.
1116. *Trifolium arvense* L. Rabbit-foot Clover. Licking County. Robert B. Gordon.
1125. *Psoralea pedunculata* (Mill.) Vail. Long-peduncled Psoralea. "Collected at Stony Creek, State Forest, Ross County. A. E. Miller.
1149. *Meibomia marylandica* (L.) Ktz. Maryland Tick-trefoil. "Dry hillsides near Peebles," Adams County. A. R. Harper and Edw. S. Thomas.
- 1161.1. *Vicia villosa* Roth. Hairy Vetch. Escaped from cultivation. Ohio State University farm, Columbus, Franklin County. Robert B. Gordon.
- 1173.1. *Clitoria mariana* L. Butterfly Pea. "On edge of pine woods." Roosevelt Preserve, Scioto County. Arthur R. Harper.
1182. *Sedum telephioides* Mx. American Orpine. "Crevice of a steep cliff." Hillsboro, Highland County. Katie M. Roads.
- 1210.1. *Vitis cinerea* Engelm. Ashy Grape. Sardinia, Brown County; Arion, Scioto County. Collected in 1900 by W. A. Kellerman. Determined by Chas. C. Deam.
1253. *Humulus japonicus* S. & Z. Japanese Hop. Persistent after cultivation. Columbus, Franklin Co. John H. Schaffner.
- 1305.a. *Salix nigra amygdaloides*. Columbus, Franklin County. Collector, R. F. Griggs. A. D. Selby.
1312. *Salix glaucophylla* Bebb. Broadleaf Willow. Cedar Point, Erie County. A. D. Selby.
1315. *Salix candida* Fl. Hoary willow. Border of bog, Hartville, Stark County. A. D. Selby.
1320. *Salix humilis* Marsh. Prairie Willow. Georgesville, Franklin County; Neapolis, Lucas County. A. D. Selby.
- 1346.1. *Kneiffia longipedicellata* Small. Long-pedicelled Sundrops. Midland, Clinton County. "Meadows." E. Lucy Braun.

1385. *Pyrola americana* Sw. Round-leaf Wintergreen. Near Newark, Licking County. Robert B. Gordon.
1392. *Hypopitys lanuginosa* (Mx.) Nutt. Hairy Pinesap. Collected in "The Gulf." Hocking County. A. R. Harper. Also "Red Hills," Delaware County. R. B. Gordon and Irvine Wolfe.
1405. *Polycodium stamineum* (L.) Greene. Deerberry. "In pin oak woods," between White Oak and Mt. Oreb, Brown County. E. Lucy Braun.
- 1432.1. *Convolvulus fraterniflorus* Mack. & Bush. Short-stalked Bindweed. "Sandbar along lower Scioto." Scioto County. A. R. Harper.
1480. *Acerates viridiflora* (Raf.) Eat. Green Milkweed. Pike Co. A. R. Harper.
1481. *Acerates floridana* (Lam.) Hitch. Florida Milkweed. "Along roadside and in waste fields." Waverly-Minford Pike, southeast portion of Pike County. Also along Blue Run Pike, Northeastern Scioto County. A. R. Harper.
1484. *Asclepias purpurascens* L. Purple Milkweed. Near Blue Creek P. O., Adams County. A. R. Harper.
1487. *Asclepias sullivantii* Engelm. Sullivant's Milkweed. Sinking Springs Cemetery, Adams County. A. R. Harper.
1493. *Asclepias verticillata* L. Whorled Milkweed. "Pretty general on marl and limestone." Adams County. A. R. Harper.
1497. *Petunia violacea* Lindl. Common Petunia. "Occasional in fields and waste places. Abundant as a persistent after cultivation." Hillsboro, Highland County. Katie M. Roads.
1498. *Nicotiana tabacum* L. Common Tobacco. Persistent after cultivation. Columbus, Franklin County. John H. Schaffner.
1499. *Datura metel* L. Entire-leaf Jimson-weed. Spontaneous after cultivation. Columbus, Franklin County. John H. Schaffner.
1500. *Datura stramonium* L. The smooth-fruited, white variety. Persistent after cultivation. Columbus, Franklin County. John H. Schaffner.
1502. *Physalodes physalodes* (L.) Britt. Apple-of-Peru. "Edge of cornfield along road near Piketon." Pike County. A. R. Harper.
1531. *Gratiola virginiana* L., (*Gratiola sphaerocarpa* Ell.) Round-fruited Hedge-hyssop. Goshen Station, Clermont County. "Margins of ponds and wet clay." E. Lucy Braun.
1533. *Ilysanthes attenuata* (Muhl.) Small. Short-stalked False Pimpernell. Near Mt. Oreb, Brown County. "Wet places in pin oak woods and in clearings." E. Lucy Braun.
1557. *Agalinis paupercula* (Gr.) Britt. Small Purple Gerardia. "In swamp at Frankfort," Ross County. A. R. Harper.

1562. *Pedicularis lanceolata* Mx. Lanceleaf Lousewort. "Along stream near Steam Furnace." Adams County. A. R. Harper.
- 1598.a. *Myosotis virginica macrosperma* (Engelm.) Fern. Goshen Sta., Clermont county. "In mixed hydrophytic forest." E. Lucy Braun.
1612. *Verbena bracteosa* Mx. Bracted Vervain. "In cracks of sidewalk, river front." Portsmouth, Scioto County. A. R. Harper.
1615. *Isanthus brachiatus* (L.) B. S. P. False Pennyroyal. "In pasture lot." Hillsboro, Highland County. Katie M. Roads.
1624. *Scutellaria incana* Muhl. Downy Skullcap. Near Newark, Licking County. Robert B. Gordon.
1645. *Thymus serpyllum* L. Creeping Thyme. "This plant has been established in the Roads Cemetery, Paint Township, Highland County, for fifty years and every effort has failed to eradicate it." Katie M. Roads.
1672. *Laminum purpureum* L. Red Henbit. Ironton, Lawrence County. Lillian E. Humphrey. Also on Olentangy River bottom, Columbus, Franklin County. Olive R. Sands.
- 1713.1. *Anethum graveolens* L. Dill. Escaped from cultivation. Columbus, Franklin County. John H. Schaffner.
1719. *Oxypolis rigidus* (L.) Raf. Cowbane. In swamp near Frankfort, Ross County. Also near Rarden, in Adams County. A. R. Harper and Edw. S. Thomas.
1786. *Triosteum angustifolium* L. Yellow Horse-gentian. On hill-sides, Hillsboro, Highland County. Katie M. Roads.
1817. *Lobelia puberula* Mx. Downy Lobelia. Near Mt. Oreb, Brown County. "Shrub-meadow depression in 'white clay' area." E. Lucy Braun.
- 1833.a. *Rudbeckia hirta* L. Black-eyed-Susan. Form with yellow disk. Cincinnati, Hamilton County. E. Lucy Braun.
1835. *Rudbeckia speciosa* Wend. Showy Cone-flower. "Dry hillside near Serpent Mound," Adams County. A. R. Harper and Edw. S. Thomas.
- 1835.a. *Rudbeckia speciosa sullivanti* (Boy. & Bead.) Rob. Hillsboro, Highland County. Katie M. Roads.
1843. *Helianthus maximiliani* Schrad. Maximilian's Sunflower. Dallas Bog, Champaign County, South of Urbana. Frank T. McFarland.
1863. *Coreopsis tinctoria* Nutt. Garden Tickseed. "In a waste lot." Hillsboro, Highland County. Katie M. Roads.
1867. *Bidens comosa* (Gr.) Wieg. Leafy-bracted Bur-marigold. "Common in swamps and wet places." Hillsboro, Highland County. Katie M. Roads.

1876. *Polymnia wedalia* L. Yellow Leaf-cup. "On hillside between Serpent Mound and Locust Grove," Adams County. A. R. Harper. Also found near Georgesville, Franklin County, by A. R. Harper and Edw. S. Thomas.
- 1889.1. *Pluchea petiolata* Cass. Inland Marsh Fleabane. Near Mt. Oreb, Brown County. "Moist soil, pin oak, white woods, mostly cleared." E. Lucy Braun.
1906. *Solidago flexicaulis* L. Zig-zag Goldenrod. "Steep rocky hillside." Marshall Twp., Highland County. Katie M. Roads.
1923. *Solidago ohioensis* Ridd. Ohio Goldenrod. "In swamp on outskirts of Frankfort," Ross County. A. R. Harper and Edw. S. Thomas.
1978. *Kuhnia eupatorioides* L. False Boneset. "General on limestone waste places." Adams County. A. R. Harper and Edw. S. Thomas.
1979. *Lacinaria squarrosa* (L.) Hill. Scaly Blazing-star. "Stony hillsides in limestone section." Adams County. A. R. Harper.
1982. *Lacinaria scariosa* (L.) Hill. Large blazing-star. "In field along Waverly Pike, three miles south of Chillicothe," Ross County. Arthur R. Harper and Edward S. Thomas.
1988. *Elephantopus carolinianus* Willd. Carolina Elephant's-foot. "In grounds of Serpent Mound. General in locality." Adams County. A. R. Harper and Edw. S. Thomas.
- 2029.a. *Centaurea jacea lacera* Koch. Near Goshen, Clermont County. "In hay field." E Lucy Braun.
- 2029.1. *Centaurea vochinensis* Bernh. Tryol Star-thistle. Cantwell Cliff, Hocking County; also in West Jefferson, Madison County. Mrs. Bayard Taylor.
- 2035.2. *Picris hieracioides* L. Hawkweed Picris. Milford, Clermont County. "Weed in blue grass lawns and roadsides." E. Lucy Braun.
2058. *Hieracium gronovii* L. Gronovius' Hawkweed. Near Mt. Oreb, Brown County. "Drier pin oak woods, Rossmoyne silt loam soil." E. Lucy Braun.
2059. *Hieracium marianum* Willd. Maryland Hawkweed. Near Sardinia, Brown County. "Meadows." E. Lucy Braun.
2061. *Hieracium greenii* Port. & Britt. Green's Hawkweed. "On hillsides," Washington Twp., Highland County. Katie M. Roads.

THE OHIO JOURNAL OF SCIENCE

VOL. XXIV

MAY, 1924

No. 3

GEOLOGIC FACTORS IN ORGANIC EVOLUTION.*

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INTRODUCTION.

The presidential addresses delivered at the last two meetings of our Academy, that by Dr. Weiss† at Oberlin in 1923, and that by Prof. Osburn‡ in this room in 1922, both dealt with phases of the broad principle of organic evolution. It is my purpose this evening to accept the precedent thus established and speak to you from the point of view of the geologist with reference to certain problems of life development. With an audience including specialists in many scientific departments, an occasion of this sort demands the consideration of general principles or problems in which men of varied scientific interests may unite on common ground. No excuse is needed at the present time for offering the manifold enigma of life development as one of the most important fields now being cultivated by men of science. We approach the subject from many angles, but we inevitably find a common interest there.

Geologic factors in their broadest interpretation would, of course, embrace all the elements which compose the physical environment surrounding life at any time or place. Moreover, it is evident that many elements of an animal or plant association are present as a part of the organic environment solely by permission of geographical conditions. So closely interwoven are the two parts of any environment, the physical surroundings

* Retiring President's Address before the Ohio Academy of Science, April 18, 1924.

† A. P. Weiss, The Aims of Social Evolution; Ohio Journal of Science, Vol. 23, pp. 115-134, 1923.

‡ R. C. Osburn, Some Common Misconceptions of Evolution; Ohio Journal of Science, Vol. 22, pp. 173-192, 1922.

and the associated life, that the influence of the one is scarcely separable from the influence of the other and both alike may be considered as geologic factors. My topic, therefore, might be interpreted as involving a consideration of the role played by environment in the processes of evolution.

How environment operates in influencing successive generations in the evolution process is a moot question, perhaps one of the most important of all the unsolved problems with which we are now engaged. The wise student of evolution is today not nearly so dogmatic in his assertion that acquired characteristics are not inheritable as were many naturalists a few years ago. Most paleontologists have harboured a lingering hope that in some way the characteristics acquired by one generation may leave their impress upon the next generation. The record of the rocks frequently suggests the question, does environment influence the germ plasm and therefore have something to say about the nature of those born into each generation? Or does environment merely select from those born the few who are to survive because of chance adaptation to their surroundings? Although the geologic record inevitably raises that question, it is probable that no certain answer can be deduced from the study of geologic life development. The problem cannot be solved by the paleontologist because what he sees can be rationally explained on either basis. Apparently the solution must await the results of such studies as are now being prosecuted by experimenting biometricians.

Even though the paleontologist must give over the hope of finding the elusive answer to such fundamental questions as these, it is of real value for him occasionally to take stock of his information and to survey the stage upon which the drama of life has been played. The shift of scenes and change of properties has always found quick response from the actors in the play. A review of such responses at certain critical moments in the past, coupled with an attempt to explain them, may help us as we chart the course which mankind may hope to pursue through coming geologic epochs.

GEOLOGIC FACTORS IN THE ORIGIN OF LIFE.

The first appearance of living organisms upon the earth constitutes an event which will always be fraught with the profoundest interest, but which will probably ever be shrouded

in deep mystery. Almost altogether unhampered by facts, one is left free to speculate along many different avenues. Geologists and astronomers seem in general agreement concerning the likelihood that our earth has passed through a juvenile stage of growth by accretion of "planet dust." The Planetesimal Hypothesis of Chamberlin and Moulton, or some modification of that hypothesis, makes a strong appeal to all who have attempted to sketch the evolution of the solar system. Long before the earth had attained its present maturity, its surface conditions would presumably have been favorable for life as we know it today. All available data indicate that ever since the earth was of dimensions comparable to those now possessed by Venus its atmospheric constitution, surface temperatures, light intensity, etc. have been within the range of conditions under which life is known to exist.

It would be expected that no long delay would ensue after the earth became suitable as an abode for life before that opportunity would have been seized and life originated. If such was the case, living creatures have existed on the earth from a date which must be placed far back beyond the dawn of geologic history, long before the oldest known rocks were formed. The surface of the juvenile earth of that early time must now be buried hundreds of miles deep beneath the materials subsequently added to it during the final stages of organization of the solar system. The high temperature and intense pressure of the earth's interior have long since completely altered those ancient surficial rocks beyond any possibility of recognition. The vast eon of time which has since elapsed has effectively obliterated all vestiges not only of the primordial life itself, but of its terrestrial environment as well.

The only safe grounds within which speculation concerning the origin of life is justified are those which imply that the material substances from which living cells were first constructed were previously present among the rocks and minerals of the earth. Frost,* Osborn†, and others have stressed the fact that the chemical elements essential in living protoplasm

* E. B. Frost, *The Contribution of Astronomy to General Culture*; Journ. Sci. Lab. Denison Univ., Vol. 16, p. 360, 1911.

† H. F. Osborn, *The Origin and Evolution of Life*, New York, 1918, pp. 45-48, 59-67.

are among the most ubiquitous of all the elements in the universe. All the necessary ingredients were certainly present in the outer shell of the growing earth. The geologic factors involved in the accretion of planetesimal matter upon the earth's surface afforded almost limitless variety of chemical combinations. The Chamberlins,* father and son, have called our attention to the many unstable and highly complex carbides, nitrides, phosphides, etc., present in the meteorites which have reached the earth's surface during recent time. Presumably these are samples of the material added to the juvenile earth during its Formative Eon. Chamberlin† has set forth in a characteristic masterpiece of logical deduction many reasons for the belief that the pulverized and porous surface layer of the growing earth was the most probable environment in which life may have originated. The open spaces at variable depths below the actual surface of the lithosphere must have been filled by the water of the primitive hydrosphere. Except during times of precipitation, the pores in the ground in close proximity to the surface were comparatively dry. Somewhere between the water table and the surface any desired relationship of water, air, and mineral matter could have been found. Here the long, slow process of chemical synthesis, constructing the chain which led eventually to the first protoplasm, is believed to have taken place. Beyond doubt, there were numerous errors in the many trials attempted at different times and places, but opportunity was practically limitless both in time and space. If the requisite minerals were wanting at a critical point in the synthetic processes in one place, somewhere else the proper sequence might be obtained. If at one locality an unfortunate episode of volcanic activity, crustal movement, or planetesimal infall destroyed the delicate balance between the complex hydrocarbon compounds and their surroundings, somewhere else at some other time there would be no such untoward circumstances.

Chamberlin‡ and Osborn§ have both commented on the frequency with which complex hydrocarbon compounds assume the colloidal rather than the crystalline state. It is thus that

* T. C. Chamberlin and R. T. Chamberlin, Early Terrestrial Conditions that may have Favored Organic Synthesis; *Science*, Vol. 28, pp. 902-904, 1908.

† T. C. Chamberlin, *The Origin of the Earth*, Chicago, 1916, pp. 252-256.

‡ Loc. cit., pp. 255-257.

§ Loc. cit., pp. 58-59.

the inorganic world simulates its physical appearance and constitution the organic. More than likely the postulated chemical synthesis was favored by the presence of colloids in the interstices between the grains of the outer shell of that primitive earth. The suggestion has been made that the walls bounding the tiny spaces in the soil anticipated the development of cell walls inclosing the protoplasm of the primitive unicellular plant-animal.

But this is only a part of the story. Life is something more than matter. Living creatures are characterized by vital energy, something about which we really know very little, but something which is absolutely indispensable to every organism. Obviously the material constituents of life were under the sway of geologic factors. Did those same factors also determine the energy content of the ancestral cell? Abundant sources of energy of various kinds were doubtless present at and near the surface of the growing earth. Solar radiance, electrical vibrations, radioactive compounds, chemical reactions, all of these and perhaps other sources of energy were available. It is conceivable that the synthesis of vital energy paralleled in the spiritual realm, if I may use that term in a very broad sense, the synthesis of protoplasmic substance in the material realm. Here the geologic factors are so obscure that it is hardly worth while to attempt any speculation.

Chamberlin* closes his volume on the origin of the earth with the following thought-provoking sentence: "It is our personal view that what we conveniently regard as merely material is at the same time spiritual, that what we try to reduce to the mechanistic is at the same time volitional, but whether this be so or not, the emergence of what we call the living from the inorganic, and the emergence of what we call the psychic from the physiologic, were at once the transcendent and the transcendental features of the earth's evolution." With this conclusion, many geologists are in hearty accord. May it not be that life as we know it is but one manifestation of the mysterious spiritual powers which permeate the universe? The geologic factors assembled in the primitive earth provided an environment within which the spiritual could manifest itself in the material. The form which it should assume may have

* Loc. cit., pp. 261-262.

been largely determined by that environment. At the very genesis of organic evolution the physical environment presented an opportunity and suggested a method for its utilization. The primitive cell was the result.

GEOLOGIC FACTORS IN THE EVOLUTION OF MARINE INVERTEBRATES.

It is a far cry from that hypothetical first cell, the original primitive plant-animal, to the splendid array of widely deployed marine invertebrates which are recorded in the rocks of the Cambrian period. The record of that tremendous transition is almost entirely lost. The rocks of Archeozoic and Proterozoic age, the first two great eras of known geologic time, can scarcely be expected to reveal the secrets which we would like to know. But the succeeding Paleozoic era witnessed what seems to have been the greatest progress and most significant achievements of marine invertebrates. Dynasties like the trilobites reached their climax and declined almost or quite to disappearance. Organic mechanisms peculiarly devised for efficient locomotion were perfected by a vast multitude of diverse creatures. Sense organs of great usefulness were consummated by the representatives of numerous invertebrate orders. Protective devices of shell covering or other structures reached a superiority which has never been excelled. At the close of the era the assemblage of marine invertebrates was far superior in every way to the ancestral types who had embarked upon the Cambrian seas. Were there factors in the Paleozoic environment which could have been responsible for that remarkable progress?

It happens that our knowledge of Paleozoic geography and history is unusually complete. During that long interval of time the eastern half of North America was close to sea level. Successive oscillations of level from time to time changed the relations between land and sea so that great shallow embayments crept inward from the margins of the continent, inundated vast areas in what are now the eastern states, and later withdrew to the very margins of the continental platform. Schuchert in his *Paleogeography of North America** has assembled data concerning the displacements of the ocean

* C. Schuchert, *Paleogeography of North America*; Bull. Geol. Soc. America, Vol. 20, pp. 427-606, 1910.

strand line during the Paleozoic Era. His quantitative estimates of the inundated areas of North America during successive episodes of marine transgression and continental emergence are, of course, only approximations to the actual facts. The data are by no means accurate and such figures must be held subject to considerable change with increased knowledge. Nevertheless, they give a good idea of the areas involved.

The first inundation of our continent at the opening of the Paleozoic Era apparently did not exceed eighteen per cent of the continental area. It was followed by an emergence during which nearly all of the previously submerged area was above sea level. Shortly thereafter a greater transgression of the sea flooded about thirty-one per cent of the continent, and was followed by an emergence in which more than half of the inundated area became dry land. A quantitative estimate of the succeeding oscillations of land and sea may be succinctly given by quoting the figures for each of the stages which Schuchert has reported on his paleogeographic maps. The successive areas of inundation are as follows: 21%, 12%, 23%, 12%, 57%, 10%, 40%, 5%, 35%, 5%, 35%, 20%, 25%, 5%, 13%, 7%, 27%, 3%, and 1% of the present land area. Apparently these oscillations of the shallow continental seas were among the most important factors contributing to the evolutionary processes. The differences in the figures give a fairly accurate impression of the differences in area available for shallow water life. Times of sea advance and marine transgression were characterized by what has frequently been called expansional evolution. The area available for life was constantly increasing; food supplies were abundant; competition was not severe. Marine invertebrates deployed with utter abandon; every possible experiment was tried; new varieties and species appeared, almost without number. Times of continental emergence were marked by restrictional evolution. The area available was constantly diminishing; living creatures were crowded into ever closer proximity one with another; food supplies were more and more insufficient. The struggle for existence became more acute; the many experiments which had been tried during the luxurious ease of the advancing seas were now appraised and tested. Not only were the decidedly unfit creatures blotted out of existence, but in very truth only the fittest survived. The oscillations of the strand line occa-

sioned pulsations of life. Episodes of expansional and restrictional evolution succeeded one another with monotonous regularity.

Another geologic factor worked in close harmony with the changing area of the shallow sea. Advancing seas invaded each continent from several points of the compass contemporaneously. Embayments like Hudson Bay and the Baltic Sea crept in toward the center of the land areas. For long intervals these embayments were more or less completely isolated one from another. In the main, the Paleozoic seas were probably fairly uniform in temperature, but probably differed materially in salinity and turbidity. A particular embayment, therefore, might be hospitable to certain species such as are found among the molluscs, but at the same time inhospitable to other animals like the corals or the crinoids. Isthmian or other barriers from time to time may have effectively prevented the invasion of an embayment by many forms of life inherently suited to its conditions, and thus have isolated its local population from foreign immigration. For these and other reasons, provincial faunas characterized many Paleozoic epochs.

Each province had its own assemblage of plants and animals, set in a physical environment more or less peculiar to itself. In an attempt to cope with its own special problems, each phylum would perfect its own adaptations. Equilibrium within the province would be attained. Creatures favorably adapted to the local situation would develop. Continued transgression upon the land at many times resulted in the coalescence of hitherto isolated seas. An embayment from the Mackenzie valley, extending southward across Iowa into Illinois, might there become confluent with an embayment from the Gulf of Mexico, extending northward across Mississippi and Tennessee and reaching likewise into Illinois. As a rule, at the climax of sea transgression there was much commingling of the waters of previously separated gulfs and bays. The result is obvious. Provincial faunas mingled with each other and invaded territories from which they had earlier been barred. Life quickly assumed a cosmopolitan aspect as the old barriers were broken down. Again there was abundant opportunity for appraisal of results. Experiments which had proved successful in one embayment were now compared with the best that had been

achieved in another province. The creatures selected in the earlier elimination trials were now pitted against each other in the championship meet. The cosmopolitan type would be characterized by the best possible selections from the many provincial units.

This shifting emphasis from provincial to cosmopolitan faunas must frequently have coincided with the change from expansional to restrictional evolution. The two factors were closely allied. Together they must have contributed tremendously to the sifting processes. The earlier part of an ideal period of the Paleozoic Era would be marked by slowly advancing seas and expansional evolution. The middle of such a period would witness the climax of expansional development and the mingling of provincial faunas to provide the cosmopolitan type. During the later part of the period, retreating seas would carry toward the continental margins the dwindling remnants of the cosmopolitan faunas. These were times *par excellence* of testing and appraisal. Such pulsations as these in environment and life seem to have provided both the necessity and the opportunity for progressive development among marine invertebrates.

The case is particularly clear for animals of that type in the Paleozoic seas, but it is apparent that similar geologic factors have contributed toward the progress of many organisms at all times. Nature thus provides opportunity for the "ceaseless urge" within the organism to experiment with all possible methods of achieving success. Then come the times of testing, when the results of these numerous experiments are weighed in the balance, one against the other. Here is one of the most significant contributions which geologic factors have made to organic evolution.

GEOLOGIC FACTORS IN THE EVOLUTION OF FISHES.

The first known record of vertebrate life is contained in rocks formed during the second period of the Paleozoic Era. The record is a fragmentary one, but it indicates creatures ordinarily interpreted as primitive fish-like forms. The relics are, however, so obscure that they do not give much of a clew to the solution of the problem concerning the origin of vertebrates. In the present inquiry, however, we are not concerned with the missing link between the first vertebrates and their

invertebrate ancestors. Rather we are interested in the environment which favored the development of the higher type of life. Chamberlin* has again given us the advantage of his clear perception of the factors involved. He calls attention to the characteristic distinction between the body form of fishes and that of most other aquatic creatures. He suggests that it is this body form, presumably devised in response to a particular environment, which is the real achievement of these most lowly vertebrates.

To summarize his conclusions, it may be stated that the geologic record contains strong implications that fishes did not originate in the sea. The fragmentary record above referred to is contained in rocks which have been interpreted by many observers as deltaic in nature. The fragments of fish teeth, plates, and bones embedded in the muds and silts, presumably had been transported down a river and thus suffered considerable attrition before they came to rest. The first record of marine fishes, occurring near the close of the next succeeding geological period, decisively indicates long antecedent evolution to account for the wide deployment into diverse orders which had already been accomplished. The complete absence of all ancestral types from the richly fossiliferous marine strata of the earlier Paleozoic periods may be explained only in two ways. Either fishes had been developed in the waters of the land or in some remote and at present altogether unknown sea. Most paleontologists incline to the former view.

“There is only one conspicuous type that is facilely suited to free life, independent of the bottom, in swift streams, and that is the fish-form. The form and the motion of the typical fish are a close imitation of the form and motion of wisps of water-grass passively shaped and gracefully waved by the pulsations of the current. The rhythmical undulations of the lamprey which perhaps best illustrates the primitive vertebrate form, and is itself archaic in structure, are an almost perfect embodiment in the active voice of the passive undulations of river confervæ. The movement of the fish is produced by alternate rhythmical contractions of the side muscles, by which the pressure of the fish’s body is brought to bear in successive waves against the water of the incurved sections. In the

* T. C. Chamberlin, On the Habitat of the Early Vertebrates; Journ. Geology, Vol. 8, pp. 400-412, 1900.

movement of a rope of vegetation in a pulsating current, it is the pressure of the pulses of water against the sides of the rope that give the incurvations. The two phenomena are natural reciprocals in the active and passive voices.

"The development in the fish of a rhythmical system of motion responsive to the rhythm impressed upon it by its persistent environment and duly adjusted to it in pulse and force, is a natural mode of neutralizing the current force and securing stability of position or motion against the current, as desired. Beyond question, the form and movement of the typical fish are admirably adapted to motion in static water and that has been thought a sufficient reason for the evolution of the form, and so possibly it may be, but fishes in static water have not as extreme lateral flexibility as have those of running water."*

This very logical explanation of the development of fishes as a response to the environment afforded in swift-flowing streams is of course quite hypothetical. In the present state of knowledge, we have no data adequate either to prove or disprove the theory. It nevertheless opens up a stimulating trend of thought and is in harmonious alignment with deductions made at various other strategic points in life development. Apparently, here as elsewhere, the geologic factors not only set a problem for life to solve, but also whispered a suggestion as to the method of solution.

GEOLOGIC FACTORS IN THE RISE OF TERRESTRIAL VERTEBRATES.

The emergence of air-breathing quadrupeds from the aquatic environment in which live the gill-breathing and finned fishes constitutes one of the most dramatic events along the road leading toward man. Apparently that event occurred shortly after the middle of the Paleozoic Era, for in the later Paleozoic rocks there are abundant footprints and frequent skeletons which indicate the presence of amphibians and reptiles.

Barrell has made a critical study of the geologic factors involved in this particular episode of organic evolution. From his own summary of his paper,[†] entitled "The Influence of

* T. C. Chamberlin, loc. cit., pp. 407-8.

† J. Barrell, Bull. Geol. Soc. America, Vol. 27, pp. 387-436, 1916.

Silurian-Devonian Climates on the Rise of Air-breathing Vertebrates," the following paragraphs may be quoted.

"The amphibians are represented in the later Paleozoic by certain skeletons preserved in the accumulations of coal swamps, but more abundantly by footprints in formations having the character of semi-arid flood plain deposits. As the record is traced backward, the skeletons disappear, and the oldest abundant traces are footprints left in shales and sandstones, chiefly red in color, of Lower Carboniferous age. These are the deposits of rivers which were in the main subject to seasonal shrinkage in markedly semi-arid climates. The footprints lead us back to the habitats of river fishes, the ancestors from whom they sprang. There are here converging lines of evidence that the rise of amphibians came not from the sea, but from the land waters. The exposure of the tidal zone alternately to water and to air had, then, nothing to do with the origin of lungs.

"Having made this study of environments, the argument passes on to an analysis of causes leading to the rise of amphibians. The law of probabilities shows that the directive influence of external factors is necessary to guide the development of old organic structures into combinations of new structures which shall be efficient under a combination of new conditions. Natural selection, although not now regarded as an explanation of most minor organic variations and the development of new species, is nevertheless a broad controlling force which compels development within certain limits of efficiency. What, then, were the causes which controlled the passage of fishes into amphibians? The chief cause is found to have been the nature of Silurian and Devonian climates. The warm and stagnant waters of the dry season compelled those fishes which should survive to make larger and larger use of air. The organic nature of fishes was at that time happily able to vary in pace with the demands of changing environment.

"The evidence is regarded as strong that the air-bladder was originally developed as a supplemental breathing organ, although in modern fishes it has been mostly diverted to other uses. Among certain Devonian fishes, living under more and more strenuous climatic conditions of seasonal dryness, the use of the air-bladder for respiration became essential, and with the diminishing availability of the waters of certain regions the

gills in those species which survived this crisis in evolution became correspondingly atrophied. The amphibians thus arose under the compulsion of seasonal dryness.

“In conclusion, it is noted how the particular method of accessory respiration which was adopted by the ancestors of amphibians was only one of several methods which have been used by fishes. This method of accessory respiration permitted the rise of land vertebrates and determined the future lines of evolution, but another choice of the mode of respiration might have led to more rapid progress—a progress which would, however, have been directed into somewhat different lines.”

Barrell thus concludes that “climatic oscillation is a major ulterior factor in evolution.” Again, a geologic factor may be observed to play an important directive part in the drama of life development. The necessities imposed upon the organism because of certain peculiarities in the environment formed a problem which was not impossible of solution. The upward step involved in the evolution of amphibians from fishes was occasioned by local and temporary geologic factors. No ultimate goal could possibly have been even fleetingly envisioned by ambitious fishes. To be sure, the successful achievement of air-breathing apparatus permitted later generations of creatures to progress far by numerous subsequent steps, but the future possibilities were not in the least involved in the momentary crisis. Creatures inherently possessing qualifications which made possible the development of primitive lungs were for the moment set in an environment which stimulated that achievement. The result was of far-reaching consequence to all life.

GEOLOGIC FACTORS IN THE ADVENT OF REPTILES.

The outstanding biologic event of the closing Paleozoic periods was the improvement of terrestrial vertebrates until the reptilian stage was reached. The fossil record shows a nearly complete transition between certain amphibians and the more lowly reptilian orders. No such pronounced structural differences as now separate these two classes of vertebrates were present in late Paleozoic time. In its simplest statement, this forward step in life development involved two changes, both of which were necessary to liberate land animals from the necessity of retaining close contact with their ancestral aquatic

environment. In the first place, the individual's metamorphosis from the gill-breathing to the lung-breathing stage must take place sufficiently early in the life history of the creature to be complete by the moment of birth. Otherwise, the young must be hatched in the water. In the second place, the egg must be so constructed as to permit its incubation in the air rather than in the water.

Lull* has interpreted these changes as a response to a climate becoming progressively more and more arid. He suggests "that whereas semi-aridity with seasonally recurring rains impelled amphibian evolution, true aridity with undependable rains making amphibian economy impossible stimulated the evolution of the reptiles." This explanation is in perfect harmony with the known facts concerning the extension of wide desert areas in what are now the southwestern states, at a time which is approximately contemporaneous with the first records of true reptiles. It happens that some of the very oldest reptile remains are found in the Coal Measures of Illinois, in strata whose composition clearly indicates the presence of marshes and swamps of so vast dimensions as to have been possible only in a humid region. These were, however, coincident in time with vast arid deserts at no remote distance toward the south and west, and it might well be expected that the early reptiles soon sent expeditionary forces from their birthplace in the desert to the adjacent humid lands with their greater wealth of food resources.

Case† has made a paleogeographic study of the environment of North American vertebrates in the Late Paleozoic. He concludes from the available data that the development of vertebrate life at that time "emphasizes the changes from a long period of slow evolution in a singularly monotonous environment through a period of rapid expansion in a diversified environment" resulting in the final extinction of most of the life strains involved. "The chief directing influence in the sudden expansion was a decided climatic change, accompanied by physiographic changes, induced by an alteration in the level of the surface of the continent." The Pennsylvanian period was the next to the last in the Paleozoic Era and was

* R. S. Lull, *Organic Evolution*, New York, 1917, pp. 494, 5.

† E. C. Case, *The Environment of Vertebrate Life in the Late Paleozoic in North America*, Carnegie Inst., Washington, D. C., pub. 283, 1919.

succeeded by the Permian period. During Early Pennsylvanian time, the geologic factors surrounding North American life were singularly uniform over most of the continent. Apparently there was an equably humid climate; great areas of the continent were approximately at sea level, so that wide marshes and swamps were an almost constant feature of the landscape. The ultimate food supply, vegetation, was abundant in quantity and an enormous number of animals must have found easy subsistence. The air-breathing vertebrates were still in the first stage of their development—the stage of youth, with all its resiliency, flexibility, and readiness to experiment. But amphibian development seems to have been especially slow. Case suggests that the monotony of the environment restricted the progress which might otherwise have been expected. The vertebrate fauna was, however, “accumulating force towards a great radiation to be expressed as soon as the limitations were removed even in a partial degree.” This was apparently one of several long periods of stagnation in evolution which were followed by rapid development, an association so frequently noted that Case records his “impression that faunas in periods of stagnation go through a period of preparation in some form for their subsequent radiation.”

Toward the end of the Pennsylvanian period, far-reaching physical changes began to make themselves apparent throughout North America. In general, there was a gradual elevation of the land, accompanied by changes to a cooler and less humid climate. Swamps and marshes dwindled to disappearance. Wide sandy wastes extended over large areas in both the eastern and western half of the continent. Red beds appear among the upper strata of the Coal Measures, and throughout Permian time rocks of that nature were the dominant type in most parts of North America. “The fauna, long restrained from any expression of its evolutionary tendencies, full-fed and in the vigor of its youth, responded at once to the change, and new forms appeared so suddenly as to be unheralded in the preserved remains.” Reptiles made their appearance in considerable force and promptly took command of the available lands. Their deployment into diverse strains was especially rapid and was no doubt a response to the varied opportunities of the notably diversified environment. The strange and mysterious fin-backed lizards, the graceful, slender, swift-moving *Areoscelis*,

and the efficiently aquatic mesosaurs are suggestive of the products of three of the many lines of evolution which were pursued.

Somewhat similar climatic and physiographic conditions maintained in South Africa at that same period in earth history. There, also, the reptiles took advantage of the congenial surroundings and the new opportunities. Progress was along very similar lines. But at that locality, one reptile strain showed tendencies which foreshadow the evolution of mammals. So far as the fossil record goes, these tendencies are most apparent in the teeth and skulls. We know nothing definite concerning the progress toward the two truly mammalian characteristics, the utilizing of a portion of the energy derived from food to keep the body temperature above that of the surroundings, and the development of mammary glands for suckling the young. It is, however, within the bounds of probability that both of these mammalian characters were anticipated among therapsid reptiles at that time. If so, it was doubtless a response to another climatic change and thus indicates anew the controlling and directing influence of geologic factors.

The progressive diversification of climate during late Paleozoic time reached its climax with the arrival of a great ice age. In fact, the available evidence would indicate that the late Paleozoic glaciation marked *the* great ice age, for its glaciers were considerably more extensive than those of the much more recent glacial episodes which we commonly designate by that proud term. Regardless of comparisons, during this time of early evolution among the reptiles, there were repeated refrigerations of climate which caused ice sheets to invade the margins of the tropical zone in Africa, South America, and possibly elsewhere. It was at this time that mammal-like characters make their appearance among certain of the reptiles. It was shortly thereafter that the first creatures ordinarily interpreted as mammals left their scanty record in the rocks.

Obviously, diversification of climate, aridity here, glaciation there, are recurrent episodes in the later history of the earth. The opportunity which such climatic factors give for progressive development among land creatures has been offered many times, but only at this critical stage in the evolution of life were there amphibians capable of responding to the growing aridity and

thus of developing into reptiles. Only at this time were there primitive reptiles buoyantly youthful, capable of responding to the adversity of progressive refrigeration by developing mechanism for the manufacture and storage of heat within their bodies.

GEOLOGIC FACTORS IN THE RISE OF MAMMALS.

The Mesozoic Era, which followed the Paleozoic, is designated as the "Age of Reptiles" because during that long interval of time, reptiles dominated land, sea, and air. The excellent start which reptiles had made in response to the changing conditions during the closing moments of the Paleozoic Era bore rich fruit in the host of saurians, peculiarly adapted to every conceivable environment, which retained chief prominence throughout Mesozoic time.

But this era is also characterized by the advent and early development of mammals. Fragmentary remains of teeth and jaws, preserved in the rocks formed during the first of the Mesozoic periods, are ordinarily interpreted as indicating the presence of egg-laying mammals of small size and in few numbers. They are beyond doubt the offspring of the therapsid reptiles whose response to the increasing cold of the late Paleozoic glacial epoch foreshadowed mammalian characteristics and blazed the trail for mammalian progress. Although there were considerable fluctuations of climatic and physiographic conditions during Mesozoic time, there were no geographic changes comparable to those which marked the transition from the Paleozoic to the Mesozoic until a somewhat similar transition occurred at the close of the Mesozoic Era. The main lines of evolutionary progress among vertebrates seem to have been blocked out at the very start of Mesozoic time, and were followed with little deviation during its successive periods. The mammals showed a remarkably slow though steady development.

Not a single complete mammal skull, much less a complete mammal skeleton, has yet been secured from Mesozoic rocks. Our information concerning the early progress of mammals is based on fragments of jaws and scattered teeth. These are ordinarily interpreted to mean that about the middle of the era, mammals similar to the marsupials of today were present. These creatures, though viviparous, possess no mechanism

for the long continued nourishment of the embryo within the body of the female. Therefore, the young are born in an extremely immature stage and are for a time carried in a pouch on the abdomen of the female. No relics which can possibly be interpreted as pertaining to placental mammals have yet been found in Mesozoic rocks. The peculiarly archaic appearance of the placentals, whose remains are abundant in the first strata of the next era, accords with the customary conclusion that placental mammals did not appear until the transition between Mesozoic and Cenozoic time.

The reasons for this apparent mammalian reluctance to develop rapidly are quite obscure. In part, their stagnation may be explained as similar to that displayed by the amphibians in the latter part of the Paleozoic Era. Mesozoic climates and geography were not nearly so uniform or static as those of early Pennsylvanian time, but on the other hand they were not nearly so varied and diversified as those which characterize the opening and closing epochs of many eras. Again, the slow progress of mammals has been explained as due to the tremendous overburden of reptilian life which temporarily dominated all vertebrate evolution. In the face of such tremendous odds, the mammals could try no new experiments and may have been quite content with their good fortune in managing to escape complete extinction. Yet, this adverse organic environment would seem a likely stimulus toward progress. What achievements were attained by Mesozoic mammals appear in large part a response to the necessities imposed upon them by their reptilian enemies. Such a typically mammalian characteristic as parental affection must have been stimulated by the necessity of protecting immature young from the depredations of the multitude of carnivorous dinosaurs and other blood-thirsty saurians. Mammalian intelligence, whether instinctive or reasoning, may likewise have been stimulated in a similar way. Frail and puny mammals could escape powerful and huge reptiles only by outwitting their more muscular opponents. Sharp wits rather than sharp claws, quickness of mind rather than quickness of limb, stood the mammals in good stead in those dark ages of reptile strength.

Attention has frequently been called to the fact that the customary food of placental mammals is directly or indirectly supplied by angiospermous vegetation. Nuts and fruits, herbs

and grains, grasses and shrubs, are the basic food resources of all modern animals. None of these were present in any abundance at the opening of Mesozoic time. Although scanty records of plants believed to be primitive angiosperms have recently been found in the late Paleozoic Coal Measures, it is certainly true that angiosperms were not present as a quantitatively important part of the flora until after the middle of the Mesozoic Era. The revolution in the flora which took place at that time did not, however, make any great impress upon terrestrial life. It is hardly possible that the lands upon which angiosperms became numerous were geographically isolated from those upon which the Mesozoic mammals were residing. Rather, it would seem that other conditions than the nature of the food supply determined the slow progress and final arrival of the higher mammals.

Mesozoic mammals were probably more or less omnivorous, with a penchant for the eggs of reptiles and birds. This may have played an important part in the downfall of the dinosaurs and other terrestrial reptiles who were presumably accustomed to depositing their eggs on the warm sands and leaving them unattended to be incubated by the heat of the sun. In any event, the fossil remains of land reptiles are mingled with ever increasing numbers of mammal jaws and teeth in successively higher strata deposited toward the close of Mesozoic time. Then came an abrupt change, a veritable revolution, affecting all the vertebrate population of the earth. The close of the Mesozoic Era is marked by the complete downfall of the reptiles and was soon followed by the advent in great force of the placental mammals. This overthrow of reptile domination cannot, however, be attributed to success on the part of placental mammals in a contest for supremacy with the saurians. Our records indicate that it was not until after the dominant reptiles had disappeared that the placental mammals appeared upon the scenes. If the downfall of the reptiles is to be attributed to the achievement of the mammals, all credit for that successful revolution must be given to the non-placental mammals of the Mesozoic Era. More likely, mammalian depredations constituted only a very minor part of the many factors involved in this significant change.

The close of Mesozoic time was marked by far-reaching physiographic changes which involved the uplift of continents

and the crumpling of strata into vast mountain ranges as well as the initiation of volcanic outbursts on an unusually vast scale. The resulting climatic changes are not known with such fullness as characterizes our knowledge of late Paleozoic climates. There may not have been so sharp a zonal concentration of tropical warmth and polar coolness as today. Yet there is some evidence which indicates that about this time, glaciers were active in British Columbia and Colorado. These may have been in high mountains or on lofty plateaus rather than close to sea level, but nevertheless their presence is significant. In all probability the crustal movements which marked the close of Mesozoic time, like those which closed the Paleozoic Era, were accompanied by marked refrigeration of the earth's atmosphere. By this time the reptiles had passed through their racial maturity and were in racial old age with all that such senility implies. Peculiarly adapted for special environments and special climates, they were unable to change their bodily structures to conform to the needs of new surroundings. Extinction of the dinosaurs, the pterosaurs, the plesiosaurs, and the ichthyosaurs was the inevitable result of changing geologic factors. Upon the stage thus vacated the placental mammals promptly appeared and with the opening of the Cenozoic Era they became the dominant type of terrestrial life.

GEOLOGIC FACTORS IN THE EVOLUTION OF TERRESTRIAL MAMMALS.

The evolution of placental mammals upon the various land areas of the several continents gives to the Cenozoic Era the designation, "Age of Mammals." Diversified climates, varied physiographic conditions, and more or less complete subdivision of lands into isolated provinces, all contributed to the wide and rapid development of the higher mammals. Matthew* has assembled a multitude of pertinent facts in his study of the influence of climate upon the dispersal of mammals during this time. Numerous authors have called attention to the obvious influences of environment upon mammalian progress. One illustration will suffice to bring the general principles clearly to mind.

The progressive development of the horse family from the little, four-toed, generalized, ancestral type to the highly

* W. D. Matthew, *Climate and Evolution*; Annals New York Acad. Sci., Vol. 24, pp. 171-318, 1915.

specialized horse, rhinoceros, and tapir of today is one of the stock illustrations of the evolutionist. The evolution of the horse is clearly in the line of special adaptation to a peculiar environment. The foot has been made more and more efficient for locomotion over a smooth, regular, and rather hard surface, although the changes directed toward that end have made it less capable of travelling over loose ground and of little use for striking or grasping or any other of the varied processes for which the feet of many-toed animals are used. The increased length in the lower leg and foot have increased the length of stride without decreasing its quickness. The reduction and disappearance of the side toes and the concentration of the step on the single central toe serve to increase the speed over smooth ground. These changes in the limbs and feet made it necessary for the grazing animal to have a longer head and neck so that the mouth was enabled to reach the ground. At the same time, the record shows a change in the teeth, which have progressed from short-crowned to long-crowned. Thus the animal has been enabled to subsist on the hard, comparatively innutritious grasses of the dry plains, which require much more thorough mastication than do the softer green foods of the swamps and forests. "All these changes in the evolution of the horse are adaptations to a life in a region of level, smooth, and open grassy plains such as are now its natural habitat. At first the race was better fitted for a forest life, but it has become more and more completely adapted to live and compete with its enemies or rivals under the conditions which prevail in the high, dry plains of the interior of the great continents."*

So complete is the array of fossil specimens which show the various steps in this particular progressive development and so striking is the evidence that successively more equine animals lived in successively more recent time, that there is a strong tendency to interpret the history of the horse in terms of a certain kind of orthogenesis. The interpretation of some is represented by the frivolous little verse which finds its place in every paleontologist's anthology:

"Little Eohippus was no bigger than a fox,
And on four toes he scampered over Tertiary rocks.
'But,' said little Eohippus, 'I am going to be a horse,
And on my middle fingernails to run my earthly course.' "

* W. D. Matthew, *Evolution of the Horse*; American Museum, Nat. Hist., Guide Leaflet No. 36, p. 29, 1913.

Recalling the progressive development of many organic phyla, which seem to have moved directly toward a modern type, it is very easy for us to assume that the earlier members of the phylum were possessed of impulses directing them toward the attainment of a definite though distant goal.

As a matter of fact, of course, little Eohippus had no information concerning the characteristics of the noble steed which was to be his Pleistocene descendant. His highest ambitions were presumably to escape from the stealthy approach of an ancestral feline and secure for himself safe pastures on the western prairies. To understand the straightforward progress of the odd-toed, hoofed mammals, culminating in the modern horse, one must know the changing environment which accompanied the organic modifications. During the Age of Mammals, that portion of North America which we call today the Great Plains was undergoing a radical alteration. In early Tertiary time that region was low and moist, with many swamps and widespread forests. Apparently the cordilleran barrier between it and the moisture-laden winds of the Pacific was much lower than it is today. The physical record during Tertiary time is marked by a progressive desiccation and cooling of that area. This may have been in large part a response to the building of mountain barriers at the west, although it was undoubtedly due in considerable degree to changes in the earth's atmosphere which were bringing about a more pronounced zonal distribution of temperature. Whatever may have been the causes, it is clear that the evolution of the horse family paralleled an environmental change from forested lowlands to grassy prairies and treeless savannas. This seems to have been the directing influence. Each improvement of the ancestral horses in strength and efficiency of limb, in perfection of hoof, and in effectiveness of grinding teeth, seems to have been a response to demands made by the changing environment. The four-toed, and many of the three-toed, horses were forest dwellers accustomed to browsing rather than grazing, living on the soft, springy forest mold rather than the hard, unyielding turf of the prairies. The gradual diminution of the area of forests and the expansion of the prairies not only gave the opportunity but directed and impelled the achievement of the modern type of horse. Orthogenesis seems to be a response to progressive changes in environment rather than to definite ambitions with which a creature may be endowed.

GEOLOGIC FACTORS IN THE EVOLUTION OF MAN.

Although the main outlines of the story of man's origin through modification from an arboreal anthropoid ancestor are well known, many of the details of interest in this connection await discovery. Many students of this problem have inferred that south-central Asia was the region in which this development took place, but the inference is based as much on lack of knowledge as upon deductions from known facts. One must confess that Hrdlicka's contention that east-central Europe may have been the birthplace of mankind is well within the bounds of possibility. Regardless of our lack of knowledge concerning the locality, there is no doubt but that the ancestry of man is traceable through a strain of anthropoids which gradually changed their habits from those associated with life in trees to those made necessary by life on the ground. Barrell* has sketched an interesting picture of environmental changes in south-central Asia which he believes directed that modification of the "ape-man." Gradual desiccation and increasing cold are supposed to have caused a progressive dwindling of the forest areas north of the Himalaya Mountains. The treeless steppes of the northland expanded southward, and encroached more and more upon the wooded regions. Retreat toward the south was supposedly cut off by the new-formed barrier of the impassible mountain range, and necessity forced upon the arboreal anthropoids their modification to terrestrial life. It is fairly well established that the record of man's ancestry must have included some such modifications of habits and body structures, and these are much more likely to have been imposed upon the creatures by the external compulsion of environmental changes than to have been a response to ambitions innate within the anthropoid breast.

Every section of human history bears the unmistakable stamp of the geographic environment in which man progressed from primitive barbarism to the complex civilization of today. Geologic factors are the warp without which the tapestry of human progress could never have been woven. A single illustration will serve to suggest the close relationship between man and his environment. Miss Semple has called attention

* J. Barrell, Probable Relations of Climatic Change to the Origin of the Tertiary Ape-man, *Scientific Monthly*, Vol. 4, pp. 16-26, 1917.

to the intimate relations which exist between marine highways and the later stages of human culture. "The progress of history has been attended by an advance from smaller to larger marine areas, with a constant increase in those manifold relations between peoples and lands which the water is able to establish. Every great epoch of history has had its own sea, and every succeeding epoch has enlarged its maritime field. The Greek had the Aegean, the Roman the whole Mediterranean, to which the Middle Ages made an addition in the North Sea and Baltic. The modern period has had the Atlantic, and the twentieth century is now entering upon the final epoch of the World Ocean."*

The Caucasian race, reaching the shores of the inclosed or marginal seas which form the eastern Mediterranean, found there the nursery in which were taken the first feeble steps toward the conquest of the water. Success in that limited environment was followed by the opportunity to pass into the kindergarten of the open Mediterranean. With sharpened wits and strong hearts resulting from the lessons learned in that kindergarten, the white races were ready a little later to embark along the shores of the eastern Atlantic, and in the training school afforded by its embayments, coastwise navigation was perfected. Ere long, intrepid navigators matriculated in the college of the open Atlantic; and today their successors pursue post-graduate courses in the University of the World Ocean. Again, the story of life development is phrased in terms of capable individuals presented with opportunities inherent in particular environments. Had the outlines of all the continents been like those of Africa, one can but wonder if giant ocean liners would have been a product of the twentieth century or whether they must have awaited some far distant future time.

Any broad survey of the strain of life development leading to man as we know him today can not fail but impress us with the unique succession of felicitous events which in the last analysis are dependent upon the internal conditions and external relations of the earth itself. Progress from simple to complex, from lowly organisms to higher types, from primitive conditions to "better things," is by no means a necessary consequence of

* E. C. Semple, *Influences of Geographic Environment*, New York, 1911, p. 311.

life. The ceaseless urge within the living creature appears to be only an impetus making for change. Variation may be in any direction, for better or for worse. Environment and environmental changes seem to be the directive influences. It is hardly to be expected that another planet, even among the myriad planets which may pertain to the stellar galaxy, should have had a geologic history sufficiently similar to that of our earth to have developed life along similar channels. Although there is no apparent reason for assuming that life as we know it represents the only possible manifestation of the great mysterious vital forces inherent in the spiritual universe, here is a strong argument that man is actually unique both in time and space. The law of probabilities almost excludes the possibility that anywhere else or at any other time vital energy has manifested itself in protoplasm and that protoplasm has been led through the long chain of upward progress to a creature which would be even an approximate duplicate of mankind.

If geologic factors have thus directed the history of life development and thus in a very real sense are responsible for the coming of mankind, there is no escape from the conclusion that the future history of man will likewise be under the sway of environmental factors. The key supplied by knowledge of the past is the only key available with which to unlock the door of the future. Man, a product of environment, may boast about the success with which he has subdued the earth, but the quiet power of the constantly operative geologic factors continues to define the limits within which his future activities must be set. The geologist has reason to be very optimistic concerning the possible span of the future existence of the earth as an abode for life. "While there is to be, with little doubt, an end of the earth as a planet, and while perhaps previous to that end conditions inhospitable to life may be reached, the forecast of these contingencies places the event in the indeterminate future. The geologic analogies give fair ground for anticipating conditions congenial to life for millions and tens of millions of years to come."*

Man, so far as we can tell, is unique among all animals in the possession of a definite moral purpose, a purpose to utilize to the fullest his potential ability for the "higher good." That

* T. C. Chamberlin, *A Geologic Forecast of the Future Opportunities of Our Race*; Science, Vol. 30, pp. 937-949, 1909.

higher good in its ultimate materialistic aspect means simply the continued occupation of the earth by humankind for as long a period of time as possible. With such thoughts in mind it is obviously well worth while to inquire into the place in which we find ourselves in the year 1924 when viewed in the long perspective of the whole existence of man as an animal species set in a peculiar if not unique geographic environment.

Homo sapiens is still a youthful species. His present span of life is measurable by some such figure as forty thousand years. The total span of existence of the individual species of air-breathing vertebrates has probably averaged three or four hundred thousand years. Our knowledge of the antiquity of many existing species of vertebrates indicates that among the present population of the lands, man is distinctly a newcomer. He has not yet lost the plasticity and virility of youth. He is still in the adolescence of the species and has not yet settled down into the conservatism and inflexibility of racial maturity.

The youthful species has been passing through a stage of provincial development and is even today embarking upon a more cosmopolitan career. The spread of mankind over the habitable globe has placed different individuals in diverse and isolated environments. Each continent has developed its own racial varieties. Each geographic region has witnessed the evolution of racial subdivisions having each its own distinctive characteristics. The differentiation of mankind into scores of ethnic strains has doubtless been directed in no unmistakable degree by the diversity of environmental conditions which man has found in the progressive peopling of the lands. But the last three centuries have witnessed the breaking down of barriers. Mountain and sea, forest and desert no longer serve to separate human provinces. Distance has been annihilated; barriers have been surmounted; isolation is today well nigh impossible.

Man has utilized his best ingenuity and greatest strength in an attempt to mold his geographic environment toward a uniform type. Deserts are irrigated; swamps are drained; forests are cut down; scattered clumps of trees are carefully planted and nurtured on wind-swept savannas. As a geographical agent, man works consciously toward uniformity. The world is fast becoming a neighborhood. In consequence, differentiation is waning almost or quite to disappearance.

Racial fusion or assimilation is now taking the lead. The provincial types are mingling and modifying into the cosmopolitan. For man, as for every other creature, that transition from provincial to cosmopolitan types is a time of appraisement and testing. The products of the varied provinces are now balanced against each other. The least fit must inevitably be submerged, while the more efficient and better qualified contribute largely to the final product.

But that does not mean that the most selfish, most powerful, most numerous, or even the most clever of the varied human types, from which selection is even now being made, will be the type for cosmopolitan humankind. The strain that leads to man has been clearly characterized by an increasing breadth and depth and strength of the cooperative spirit. Back at the dawn of human history, when our anthropoid forefathers maintained a most precarious existence among carnivorous mammals, to whose depredations they were exposed more and more frequently as the comparatively safe haven of the forests disappeared from the expanding prairies, the necessity of cooperation for attack and for defense was ingrained in every human survivor. The social history of man is marked by constant increase in the unit within which cooperation is workable. Family life has been submerged within that of the clan; clans were associated into tribes; tribes, into nations; nations, into alliances and leagues. Note how the geologic factors impose upon the future progress of mankind far greater and more intelligent cooperation than has yet been attempted.

Human development has thus far been marked by expansional evolution. There have always been vacant lands available for settlement, when the constant press of growing population made necessary the expansion of a community by migration or colonization. Only in times of war or in such communities as the densely populated valleys of India or China has mankind in large units ever faced the absolute necessity of conserving with utmost frugality all available food supplies. It is perfectly possible today, as it has always been in the past, for mankind to secure an abundance of food for every member of the human family. All that is required is a reasonable amount of industry and an intelligent distribution of products. But this period of expansional evolution cannot continue many centuries longer. For man, as for Paleozoic invertebrates, the

tide must turn. Expansional evolution will give way to restrictional development. Exactly how many billion human souls may find sustenance upon our earth no one can accurately estimate, but that there is a limit to the possibilities of the earth as an abode for human beings, no careful thinker who does not blink at facts can possibly deny. The limit may be as low as four billions, or as many as ten, but somewhere there is a deadline.

Far back at the very beginning of life development upon our earth, man's remote Protozoan ancestor sacrificed the ability to utilize the energy of the sunlight and make food for itself from inorganic compounds. That sacrifice bore rich fruit in the deployment and perfecting of animals of all sorts. Not the least of its consequences is just now being impressed upon mankind in the compulsion toward cooperation. Dependent upon other organisms, in the last analysis, plants, for sustenance, the future generations must conserve all available food supplies and develop to the utmost a thoroughly reliable and adequate network of transportation facilities. Mutual interdependence will become more and more apparent as the total population approaches more and more closely its ultimate limits.

How many generations will elapse before the present sixteen hundred million people on the earth have multiplied until the population reaches its absolute maximum, no one can tell. Decreasing death rates and decreasing birth rates can scarcely be balanced accurately one against another. The conquest of the tropics is well begun, but the conquest of polar lands has only recently been suggested. Very possibly, amelioration of climate with increasing chronologic distance from the last ice age may appreciably expand the areas available to serve as man's domain. Even within a few hundred years, considerable changes in the earth's atmosphere, due to man's activity in this industrial age, may react favorably by causing further diminution of arctic and antarctic ice fields. Turning from the long perspective of the many tens of thousands of years since the Cro-Magnon race of *Homo sapiens* lived in southern Europe, the few centuries which remain before the earth will have been completely populated by mankind seem to the geologist extremely short.

From the geologic point of view, therefore, the next great crisis in life development is even now imminent, relentlessly

forced upon us by geologic factors. The success with which living creatures have weathered every such crisis in the past is fair ground for optimism that this crisis of tomorrow will likewise be successfully negotiated. As in the past, so in the future, success comes because a minority respond to the challenge flung by environmental factors. The pioneers of progress have invariably been a hardy, risk-taking group, endowed with specific virtues which gradually make their way against an overburden of opposition.

Survival values in the past have generally been measured in terms of physical adaptation; survival values in this coming crisis will apparently be psychical rather than physical. Man is unique among animals in several ways, not the least important of which is the fact that he has specialized not along the line of adaptation to any one environment, but along the line of adaptability to all environments. His physical adaptability almost rules out of consideration the physical factors as determiners of survival value. Apparently, therefore, the qualities which will determine man's ability to negotiate successfully this next great crisis in life development will be psychical—mental, moral, and spiritual. Willingness to co-operate with his fellows, coupled with intelligence in devising cooperative ways and means, will be the measure of man's fitness individually and collectively to survive.

CONCLUSION.

The geologist, fresh from his survey of geologic factors in life development, has every reason to take an optimistic outlook for the future of mankind. As the twig is bent, so the tree is inclined. Geologic factors in the past have directed life onward and upward to its present high plane. A physical organism has been perfected to such a degree that it possesses a knowledge of moral law, a sense of rightness, a confidence that its reasoning mind finds response in a rational universe, and a hope that its spiritual aspirations will find increasing answer in a spiritual universe. Intelligent enough to read the record of the past and face the problems of the present, it is inconceivable that man should fail as he attempts to develop within himself a spirit of cooperative endeavor strong enough and intelligent enough to insure his success in the critical moments of the future.

PRINCIPLES OF PLANT TAXONOMY. I.*

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In 1905, the writer began publishing a series of papers on the phyletic classification of plants, which gave a general arrangement of the entire plant kingdom and also a discussion, in an elementary way, of the evolutionary facts on which a true classification must ultimately rest. These papers appeared in THE OHIO NATURALIST and its continuation as THE OHIO JOURNAL OF SCIENCE. No. I appeared in Vol. V, 1905; Nos. II and III in Vol. VI, 1905-6; Nos. IV and V in Vol. IX, 1909; Nos. VI and VII in Vols. XI and XII, respectively, 1911; Nos. VIII, IX, X and XI, in Vols. XIII and XIV, 1913; and No. XII, after a long hiatus, in Vol. XXII, 1922.

It is now the intention to publish a new series with special emphasis on the facts which appear to be of importance in determining a correct, evolutionary arrangement and phylogenetic classification. Some of the material given in the previous papers will not be repeated, but some of it will be considered and restated in the light of a more complete knowledge of plants, acquired by the writer through his own efforts and those of other investigators. The subjects treated will be taken up more or less at random, sometimes presenting a general aspect of the subject and sometimes a special case considered in detail.

THE SEVEN FUNDAMENTAL DIVISIONS OR SUBKINGDOMS.

In order to obtain a correct background for any scheme of classification, it is of the greatest importance to discover what have been the main movements and evolutionary advancements that have taken place in passing from the lowest to the highest types. Without reference to any notion of phyletic relationship, what is the general nature of the various types of higher and higher plants as one takes a general view of the whole plant kingdom? Such a view presents seven definitely marked stages

* Papers from the Department of Botany, the Ohio State University, No. 147.

or subdivisions, no more and no less; and each higher division is characterized by the acquisition of fundamentally new properties and activities, which result in new complexities in the life cycle, physiological processes, and structures. At each of the six transition stages some fundamental property or relation is added which is retained, after that, throughout all succeeding stages and is very rarely lost in individual cases. The emphasis will be placed on fundamental processes and physiological relations rather than on structures, as has usually been done, for it has become plain that the structures developed in any individual result from the presence of hereditary factors through the physiological activities of the cells in the given environment. In placing the emphasis on fundamental properties and functions, our classification will appear in a clearer light as simply a systematizing of the evolutionary progressions, and a more or less correct chronological arrangement of the more and more complex heredities that result in new activities, interrelations, and structures of cells and organs as one passes up the ladder of organic forms. There are, of course, morphological characteristics which delimit the subkingdoms very distinctly except the two lowest, which are separated on purely physiological grounds, since the lowest sexual forms show no dimorphism even in the gametes. But as stated above, the morphological characters are in the end merely the result of activities dependent on the presence of a given heredity in a given environment, and by emphasizing morphological features in the segregation of the great progressive divisions the attention is diverted from the main point of importance and interest. It is also possible to define the seven subkingdoms entirely in terms of their life cycles. Each group has one or more characteristic life cycles; that will clearly segregate it from all others except in the case of low forms without secondary sexual characters that have lost their sex.

The lowest plants are then apparently without sexuality. The organization of their protoplasts is apparently such that no sexual states arise under any, known conditions. These nonsexual plants include unicellular and colonial forms and multicellular forms with cell differentiation. Some might object to the recognition of these plants as a distinct subkingdom since abundant unicellular forms occur which have well-developed sexual states, but since the upward evolution of the

plant kingdom is so intimately associated with changes in the relation of the sexual state to the life cycle, it is necessary from theoretical grounds to lay emphasis on the fact that the first type of living things that appeared on the earth was apparently nonsexual and has so remained. These primitive, nonsexual plants constitute the subkingdom PROTOPHYTA.

In general, plants proceed from the unicellular to the multicellular condition, both in the ontogeny and in the phylogeny, but the transition is so gradual and involves so little change in the functional nature of the organism that it is impossible to separate the unicellular from the multicellular. In fact it is much more difficult to segregate the strictly unicellular from the strictly multicellular than to separate those with sexual states from the non-sexual. The difficulty arises because sexual organisms may fall back into such a condition that no sexual state ever develops.

In the higher forms which have lost their normal sexuality, partial or secondary sexual states arise, but in one way or another the perfect, primary sexual state is not attained and the species continues either parthenogenetically or apogamously. In the lower, unicellular and colonial species it is often difficult or impossible to form a convincing judgment as to whether the organism in question was derived from a previous sexual condition or whether it represents a direct derivative from the original nonsexual state. Such cases must be decided by a study of the complexity of the cell in general and the nucleus, and by a comparison with the nearest relatives. Usually there will be less uncertainty than there is in separating lower "plants" from lower "animals." The other five transitions offer no such difficulties. In fact with an ordinary knowledge of the morphology and life history, every species can be placed with absolute certainty. There are attraction stages in some lower organisms which in physical nature may be somewhat akin to sexuality which, nevertheless, are to be regarded as distinct phenomena not related to sexual states, namely the aggregations, fusions, or associations of cells at certain periods, as manifested in Myxobacteriales, Myxophyta, and Hydrodictyales.

In general, plants proceed from the unicellular through the colonial state to the multicellular condition, with little change in the functional nature of the organism. However, the

change from unicellular to multicellular frequently also involves a change from nonsexual to sexual, although these two evolutionary progressions are apparently due to fundamentally distinct causes.

The second subkingdom is named NEMATOPHYTA because of the prevalence of the filamentous condition in most of its classes, and because in the two succeeding subkingdoms the gametophyte usually passes through a protonema stage in its embryogeny. In this subkingdom there are three main types of life cycle: first, a simple sexual cycle with a haploid individual; second, a simple sexual cycle with a diploid individual; and third, an alternation of generations cycle with a haploid individual alternating with a diploid individual, the diploid individual being independent of the haploid individual, although in some cases a diploid, spore producing parasitic phase is present at first as in some red algæ. This alternation cycle is therefore quite distinct from the one which appears in the next higher subkingdom and which remains fundamentally unchanged to the highest plants. Each of the three life cycles of the Nematophyta may be modified in one way or another in details, the most extreme, perhaps, being the modification of the alternation cycle in such higher fungi as the rusts, where the diploid generation consists of cells with pairs of haploid nuclei rather than of cells with diploid sets of chromosomes in conjugated nuclei. Such a condition could arise if the conjugating nuclei lost, for the time being, their primary sexual states or property of attraction before coming in contact and developed it again at the end of the diploid generation stage. In contrast to the diversity of life cycles in the Nematophyta, each of the subsequent subkingdoms has but one general type of life cycle and, as stated above, all are mere modifications of one fundamental type.

The second transition in the plant series is that which leads up to the BRYOPHYTA. This is by far the greatest break or hiatus in the plant kingdom from a morphological point of view, there being no possible direct connection until one passes down to the very simple green algæ of the confervoid type. The higher green algæ have not only a different life cycle, but entirely different sexual organs. The gametangia of the Bryophytes come close in structure to those of certain brown algæ, but there is no possibility of a direct relation with this

group. So a series of hypothetical forms must be postulated for the ancestry of the liverworts and mosses. The transition to the Bryophytes marks the change from plants adapted to an aquatic habitat to those adapted to live and thrive in aerial conditions. Many Thallophytes are adapted to endure aerial conditions but usually they can only grow well during very wet periods or in very damp places, except some parasites which are, of course, supplied with moisture by their hosts. The lower types of Bryophytes are not entirely weaned from the aquatic habit, but the higher species usually show a greater and greater modification toward dry-land conditions, which finally becomes the goal of the evolutionary process. All along the line, however, there may be, here and there, a return to a secondary aquatic life. A second characteristic of the third subkingdom is the new type of antithetic alternation of generations with a permanently parasitic sporophyte. This new life cycle with its twelve fundamental, antithetic stages is retained, but evolved into a more complicated succession of intermediate stages, step by step, to the highest plants. Its presence or absence becomes a definite division line for the entire plant kingdom into Thallophytes and Meta-thallophytes. The archegonium is a new type of ovary which is barely hinted at in the Nematophyta, and the development of numerous sporocytes in a special tissue is also characteristic.

The third subkingdom, or BRYOPHYTA, may, therefore, be defined as those plants which have an antithetic alternation of generations and a permanently parasitic diploid sporophyte. The sporophyte is always homosporous. One of the most interesting developments in this subkingdom is the remarkable evolutionary advancement of the sporophyte, which passes from the condition of a simple sporangium or sack of nonsexual spores to a highly specialized individual containing a foot, stalk with a conducting strand of cells, hypophysis with true stomata and photosynthetic tissue, and a highly specialized sporangium; and in one group an intermediate growing zone, which is the first indication of indeterminate growth. Parasitism in this case has certainly not led to degeneration, but has led the way toward a condition of highly organized independent existence. By no possible stretch of the imagination could this series be considered as a reverse evolution.

The third transition, which is also a prominent hiatus, leading to the fourth subkingdom, is the consummation of the development carried forward in the evolution of the Bryophytes, namely, the change from a permanently parasitic sporophyte to a sporophyte with two distinct stages or phases in its life-history, first a juvenile parasitic stage and second a mature independent stage in which roots, true vascular tissue, highly organized leaves, and indeterminate buds are developed. The sporophyte with its indeterminate growth shows an enormous advance over the determinate sporophyte of the Bryophytes. Its early parasitic condition can properly be interpreted as being derived from a completely parasitic condition similar to that of the Bryophytes. The fourth subkingdom, or PTERIDOPHYTA HOMOSPORÆ, may, therefore, be defined as those plants with a typical alternation of generations in which the sporophyte has two distinct stages, a parasitic stage and an independent stage, and which is homosporous, the sexual state being normally determined in some stage of the development of the gametophyte. The life cycle of the Homosporous Pteridophytes, therefore, is essentially the same as in the Bryophytes, except in the peculiarity of the sporophyte having two distinct stages of existence, although the morphology of the sporophyte shows an enormous advance over the previous condition. There is no apparent ancestor among the Bryophytes, although the Anthocerotæ suggest a possible distant relationship to the hypothetical ancestors of the Pteridophytes. All plants above the Bryophytes have sporophytes with the two stages, but in some cases, of course, the second stage may be a parasite on a foreign host.

The fourth transition leading up to the fifth subkingdom is again, like the first transition, especially concerned with the sexual state. The determination of the sexual state is transferred back from the gametophyte or the spores from which the gametophyte originates to the tissues of the sporophyte generation, and as in the original evolution of sexuality, so here also, the transition appears to have occurred in a number of independent groups. Although the gap between the living Heterosporous Pteridophytes on the one hand and the Homosporous Pteridophytes on the other is small, it represents one of the most important and profound changes in the whole evolutionary progression. Below, sex is determined in haploid individuals

and above in diploid individuals. It does not seem possible that anything like a seed plant could have evolved without this preliminary step. All plants above this transition are heterosporous and always show some sexual dimorphism in the sporophyte, although in the lowest this dimorphism does not extend beyond the tissues of the sporangium and its stalk. In the extreme cases sexuality is determined in the zygote and thus the entire individual may show secondary sexual dimorphism.

Along with the transfer of the time of sex determination to the sporophyte goes a great reduction in the size and complexity of the gametophyte, which must now, of course, under normal conditions always be unisexual. This extreme reduction naturally leads to the next great transition, the development of seed plants. The PTERIDOPHYTA HETEROSPORÆ may be defined as those seedless plants in which the sexual state is determined in the tissues of the sporophyte and in which the gametophyte is greatly reduced, but is not entirely parasitic on the sporophyte, although there may be a beginning of parasitism in the juvenile stage. The life cycle becomes much more complex since there are now two kinds of sporangia, two kinds of sporocytes, and two kinds of nonsexual spores.

The change from the Heterosporous Pteridophytes to the next higher subkingdom, the GYMNOSPERMÆ, is from independent gametophytes to completely parasitic gametophytes, the spores not being shed. The female gametophyte is permanently parasitic in the megasporangium and the male gametophyte or pollen grain is at first parasitic in the microsporangium and later, on the megasporangium or ovule by means of the pollen-tube. This parasitic pollen-tube is a structure characteristic of all seed plants and along with numerous other peculiarities indicates their high position. So seed plants may be defined as those plants which have a male gametophyte with two distinct parasitic stages. Another fundamental change from the condition in the Homosporous and Heterosporous Pteridophytes is the intercallation of a resting period between the parasitic and independent stages of the sporophyte. From the liverworts on up there are, therefore, three prominent steps in the progressive evolution of the sporophyte. In the Bryophyta, the sporophyte is continuously parasitic and determinate in growth. In the Pteridophyta, the sporophyte

has an embryonic parasitic stage followed, through a gradual change, by an independent stage with an indefinite period of growth. In the Spermatophyta, a profound resting period, with a subsequent re-awakening or sprouting, is almost universally developed between the parasitic embryonic stage and the later independent stage of growth.

The typical seed plant has been completely weaned from a free water habit by taking the gametophyte from the ground and by conducting the sperms to the ovaries by means of the pollen tube. The Gymnospermæ are, therefore, the higher plants with parasitic gametophytes in which the male gametophyte falls directly into the micropyle of the ovule during pollination and thus develops a short pollen-tube, since the carpel is open and without a stigma.

It may be noted, in passing, that with the development of the seed and the resting period of the sporophyte embryo, the young sporophyte is largely taken out of the struggle for existence. It is an interesting fact that the highest plants, like the highest animals, have evolved this special care for the young of the next generation. And it is still more wonderful to contemplate all the complex changes in structures and functions that had to take place simultaneously or in close succession, in the evolution of these plants, if the complex arrangement was to work at all.

The sixth transition leading to the final or seventh sub-kingdom, the ANGIOSPERMÆ, is marked by the closing up of the carpellate leaf and the development of a stigma. Pollination is, therefore, no longer on the micropyle of the ovule but far removed and the pollen-tube is correspondingly long, having an extensive development before reaching the ovule. The second parasitic state of the male gametophyte has become highly perfected. It is interesting to note that among the ferns some groups also chose their leaflets over the sporangia. Since living seed plants were apparently all derived from the ferns it is only natural that there should be both open and closed sporophylls. The gametophytes of Angiosperms hold in general the same relations as those of the Gymnosperms, but are reduced to an extreme degree. A new development also is the process of triple fusion from which a new triploid tissue is produced beside the embryo sporophyte. This endosperm or xeniophyte is not present in the Gymnosperms, although there is occasion-

ally a fusion of the ventral canal cell with the second sperm of the male gametophyte. In a few Angiosperms more than three cells may be concerned in the formation of the initial cell of the xeniophyte. In the Angiosperms, therefore, normally five conjugating cells are in evidence at the fertilization period rather than two, as in other plants. In the Angiosperms which have primarily bisporangiate flowers with the stamens below, there is very commonly a showy perianth produced through the sterilization of the lower stamens. There is also some slight sterilization of basal sporophylls in some of the Gymnosperms, but this is never very prominent.

The transition to the Angiospermæ represents an enormous gap. There is apparently nothing so far known to indicate the line of ascent from their probable ancestors, the eusporangiate ferns. The Angiospermæ do not have any direct relation to any of the Gymnospermæ unless perhaps the Pteridospermæ. But the Pteridospermæ seem rather to be in the direct line leading up to the Cycads, Cordaites and Ginkgoes.

These then are the fundamental steps in the ladder of ascent in the plant kingdom. There are seven stages, no more and no less; for although in each of the seven subkingdoms there is a progressive advancement, this does not at any point involve a fundamental departure from established structures and functions taken by all the members, but rather a gradual advancement taken in one or more lines in the subkingdom and not marking a distinct or abrupt transition from lower to higher.

All of the higher plants are flowering plants, namely, they have their sporophylls developed on determinate axes, but the change from flowerless plants with indeterminate sporophyll-bearing axes to flowering plants takes place at entirely different levels in different groups. In lycopods and horsetails the strobilus is attained in the homosporous state. Apparently none of the ferns, either eusporangiate or leptosporangiate, and none of the quillworts evolved determinate sporophyll axes, and in the Cycadophyta the seed habit was well advanced before flowers appear. There are still two living genera of seed plants which show a flowerless condition and there is no plausible reason for supposing that they were ever any different in this respect.

In Ginkgo, neither stamens nor carpels are produced on determinate axes, although some interpret the single stamen and the single carpel as highly reduced strobili. But the latter view has little weight, for practically all the evidence points unmistakably in the other direction. In Cycas the determinate axis is a sex limited character, being developed only in plants in the male state, the carpels being produced in rosettes on the indeterminate main axis of the carpellate plant.

In the broadest sense, therefore, the presence and absence of the flower does not form a basis for grouping the higher plants into primary divisions, although after it once gets well started along the evolutionary pathway, it becomes an organ of decided progressive and segregative tendencies. It might be added that fundamentally the higher types of flowers do not differ from the lower, although as the term is popularly applied it might be inferred that Angiosperms have "flowers" and other plants do not. But there is no basis for such a notion unless the flower is defined in purely arbitrary terms.

To summarize, the evolution of the seven fundamental stages is as follows:

1. The lowest plants are non-sexual.
2. The change to the second stage is the evolution of the cell to a condition that sexual states appear from time to time, giving rise to cell conjugations and three general types of life cycles.
3. The second transition is to plants with a typical, antithetic alternation of generations life cycle with twelve fundamental stages, and with a permanently parasitic, determinate, homosporous sporophyte.
4. The third transition is to plants with a similar life cycle but having a homosporous sporophyte of indeterminate growth with two distinct stages of existence, a parasitic juvenile stage followed by an independent mature stage with roots, leaves and vascular tissue.
5. The fourth transition is to plants which have their sexual states determined in the sporophyte which thus develops, in distinct dimorphic sporangia, male producing microspores and female producing megaspores. There is also a decided tendency toward extreme reduction of the gametophyte.

6. The fifth very pronounced transition is to plants which have parasitic gametophytes, the male gametophyte having a two-phased parasitic life, the first stage in the microsporangium and the second in the megasporangium by means of the pollen tube. The sporophyte has a resting stage intercalated between its parasitic and independent phases. In the subkingdom immediately above the transition the transfer of the pollen (pollination) is directly to the micropyle of the ovule and there is no xeniophyte or true endosperm developed.

7. The sixth transition is to the highest plants with a specially developed structure, the stigma, for the reception of the pollen or male gametophyte, because of the closing up of the carpel. In consequences of this a long pollentube is developed which finally grows into the ovule. The gametophytes show the most extrement reduction and there are typically five cells concerned in conjugations during the fertilization period, a male and a female cell uniting, as in the plants below this stage, to form the initial cell of the diploid sporophyte, and a male cell and normally two cells from the female gametophyte uniting to form the initial cell of the xeniophyte or triploid endosperm. Probably universally, by a sterilization of stamens, a perianth is produced, which may be lost again through reduction.

The seven subkingdoms which form the foundation on which all plant classification must be constructed are, therefore, the following.

- VII. ANGIOSPERMÆ.
- VI. GYMNOSPERMÆ.
- V. PTERIDOPHYTA HETEROSPORÆ.
- IV. PTERIDOPHYTA HOMOSPORÆ.
- III. BRYOPHYTA.
- II. NEMATOPHYTA.
- I. PROTOPHYTA.

THE CLASS.

As shown in the discussion above, the seven subkingdoms or divisions do not represent natural or phyletic groups. In only two cases is there any direct connection between members of a lower subkingdom and those immediately above and both these transitions are in relation to the determination of sexual

states. It is because of their sharp demarkation from each other that the subkingdoms become the basis for the segregation of the fundamental major plant group units, the classes. A class is the largest, definitely determined, monophyletic group in a subkingdom. A class may be defined, therefore, as: *The largest group of plants in a subkingdom the members of which show an evident relationship to one another as compared with the members of some other group or groups in the same subkingdom.* The emphasis is to be placed on the word "evident," which involves an exercise of judgment by the classifier. Such an exercise of judgment is not required in establishing the seven subkingdoms.

In determining how great or how small a group shall constitute a "class," practical considerations should also have weight. Convenience in delimitation and definition of the group, its practical use in applied science, the advantage in not having too great a number of such units, so that they can be easily retained in the memory, and other similar considerations should be the main criteria in determining the approximate number to be established. The problem is not very different from the one in which a decision is made as to how many large or main branches a given tree with a complex branching system may have. By exercising his own judgment and adopting the work of others the writer has recognized about fifty classes. Some of these classes fall naturally into two or more subclasses and some are so large that a division into subordinate groups, higher than the order, becomes necessary for convenient treatment. These subclasses should also be limited in number for the same reasons as those given for the class. By a reasonable segregation method, the number of classes and subclasses combined falls well below the hundred mark.

With the establishment of the class as the fundamental unit which can be defined quite definitely as to its limits, the systematist has a group which becomes the basis for classification in its broadest aspects. Classes can be compared as to probable relationships and combined into the main branches or *phyla* and *subphyla* on the one hand, and on the other they can be divided into subordinate divisions, the orders.

THE SPECIES.

Just as the classes are the units in thinking and treating of plants in their general aspects and in establishing higher groups by combination or lower groups by division, so the species are the units for dealing with plants in their severalty in the science of botany in general and in all the practical relations of life. The species name, whether scientific or common, serves as a means of general communication. The species then must apply to a unit of classification which is both scientific and practical. Too great a refinement of segregation leads to an impossible system for the practical man as well as the botanist who is not especially acquainted with the given group, both because of the impossibility of definite identification and the evident impossibility of keeping a multitude of names in mind based on trivial and wholly unimportant differences. It is not the desire to attempt a definition of species here but simply to make a few practical observations. It soon becomes evident to any one dealing with diverse groups of plants that the concept for specific limits must be different for different groups, not only because of differences in the groups of organisms themselves, but also because of the special practical relations which the members of various groups sustain to mankind. In a general way, the Linnean species make suitable phylogenetic units and the term "species" should be retained for them. A serious attempt should be made to define species in such a way that the term can not be continually shifted to smaller and smaller divisions as is now being done very prominently, especially in some genera. The recognition of smaller units than the species is of great importance in certain lines of study, but definite provision should be made for lower categories within the species to any extent that may be desirable while leaving the larger Linnean units intact.

Many attempts have been made to define a species, but with only partial success. In nonsexual groups, evidently, the species can only be determined and defined by the degrees of morphological and physiological differences, but in the sexual plants, where interbreeding takes place, the species must be established on a different basis. Certainly all the forms that interbreed freely with fertile offspring are to be regarded as belonging to a single species. On the other hand, inability to

cross breed is not to be made a basis arbitrarily for species segregation, since we know that there is self sterility of the individual in many groups and often two very closely related varieties may be sterile toward each other.

In classification, the species are to be used as units of comparison in determining the next higher group, the genus. On the other hand, as intimated above, the species may be divided into smaller categories to the extreme degree, ending in the segregation of unit characters. In dividing species into smaller groups, experimental methods are to be employed; in sexual organisms for determining hereditary units, and also for determining fluctuations of ecological variations in both the sexual and the nonsexual. The study of the species resolves itself into genetic analysis on the one hand, and ecological variation or fluctuation on the other. In any freely interbreeding group, the subdivisions of the species are practically all of the same value, but for convenience standard varieties may be established based on some character or set of characters of special practical value, as for instance the consistency of the endosperm which is commonly used for segregating the main varieties of Indian corn, as pop corn, flint corn, sweet corn, etc. These endosperm characters are no more fundamental than various others that might be taken as for example pericarp colors, length of internodes, etc. But such classifications have less value from a practical standpoint. In the subdivision of economic species, therefore, the first consideration should be utility and there is no special reason why this principle should not be carried over to the non-economic species as well, wherever there is free interbreeding.

In taxonomy there are, therefore, two units of special importance, the class and the species. Both of these units must be constantly used in all studies of the evolution and classification of plants on the one hand, and in the practical application of plants in plant industry and the arts, on the other.

Since the species is considered and named in relation to the genus, the genus must also receive due consideration involving both the practical and theoretical sides. A system of names must be devised and established to insure at least a reasonable stability, otherwise the language of botany in so far as it concerns

specific names becomes burdensome and even ridiculous. It is remarkable that up to the present time there has not even been developed a system of generic types by which the names could become fairly well stabilized. It is to be hoped that this subject will now receive the serious attention it deserves from systematists.

DIMENSIONS OF THE CINCINNATI ANTICLINE.*

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HISTORICAL.

The structure mentioned in our subject was recognized in 1838 by Locke,† who was in the employ of the Geological Survey of Ohio. He was making a survey of southwestern Ohio and after examining feeble local dips "in all possible directions," he observes that "when we examine the several formations on a large scale, the true dip becomes very evident; and as one formation sinks gradually below the surface, and another superior one presents itself, they give rise to those important changes in the face and products of the country." In correspondence with Owen, of the Indiana Geologic Survey, Locke also discovered that the strata lay similarly in Indiana, but that they dipped gently westward, while in Ohio they descended eastward. The dips thus recognized were so feeble that contact instrumental measurements could not disclose them, but through careful work with leveling instruments over considerable distances the actual dips were established.

Locke does not call it an anticline, but he clearly recognizes the structure, for he says, "on ascending the Ohio River eastward (from vicinity of Cincinnati) we meet with the blue limestone, cliff limestone, slate (shale), fine sandstone, conglomerate and coal, while descending the Ohio westwardly we meet with the same things in the same order."

In 1873 Newberry‡ discussed the structure and formations in Ohio and distinctly recognized and named the Cincinnati Arch. He says its axis is through Bethel, Ohio, and its breadth in Kentucky is 130 miles, but narrower in Ohio. He adds as confirmation that "outcrops of Corniferous (Devonian) limestone, which may be said to form its base on either side, are 150

* Presented before Sec. E, A. A. A. S., Cincinnati, O., Dec. 29, 1923. Published by permission of Dr. J. A. Bownocker, State Geologist, Geol. Surv. Ohio.

† Locke, Prof. John, Geol. Surv. Ohio. Sec. Ann. Rept. W. W. Mather, 1838, p. 206.

‡ Newberry, J. S., Geol. Surv. of Ohio. Vol. I, pp. 1-103.

miles apart in Kentucky and only 50 in northern Ohio.* He also observed that east dips were stronger than those to the west, but that all were very weak, mentioning 11–40 feet per mile. He also states that there are two folds in the crest of the main structure in northern Ohio.

Robt. R. Bell, of the Canadian Geologic Survey, has reported the geanticline as far north as Lambton, Ontario, at the southern end of Lake Huron. It is very low here and cannot be traced much, if at all, beyond this point, but it has here been a very productive source of fuel. Hall† recognized the Cincinnati Geanticline or Uplift, as it is variously called, and discussed its age and relation to Paleozoic seas, but as such matters do not fall within the scope of this paper, they will be all passed over.

In 1866 Gorby‡ devoted a dozen pages to a discussion of the Wabash Arch, which is the westward branch of the Cincinnati Anticline. This westward branch, says Gorby, possesses “absolute evidence of an upheaval extending from the northern part of Indiana near the Ohio line, northwesterly by Chicago to the regions of Lake Superior.” (p. 240). He even follows a “learned paleontologist” in the suggestion that “this line or axis of upheaval is a projection of ancient disturbances, which originated in the volcanic regions of Lake Superior.” (p. 229). There seems to be no reason, however, to consider the structure beyond Kankakee, Illinois, for it is well flattened out at the Illinois-Indiana line and seems to be lost near that place.

In 1893 Cubberly§ discussed the distribution of the Trenton limestone in Indiana by means of a map and a series of sections in various directions across the state. These sections and maps were based on many drill logs. The report shows the course of the Wabash Arch. It probably divides from the Cincinnati Arch a few miles south of Cincinnati, so that its axis is recognizable at Patriot, Indiana, and may be traced northward to Brookville, where it begins to divide again. Two folds or swells, one 6–8 miles west of Richmond, and the other 5–6 miles west of New Castle, are separated by a shallow sag and fuse again

* Geol. Surv. Ohio. Vol. I, 1873, p. 99.

† Hall, James, Pal. of N. Y. 1859. Vol. III.

‡ Gorby, S. S. Dept. of Geol. & Nat. Hist. of Ind. 1886. 15th Ann. Rept., pp. 228–41.

§ Cubberly, E. P. 18th Ann. Rept. Geol. Nat. Hist. of Ind., pp. 219–255.

into one toward Muncie and Anderson and beyond to Logansport. Near Rensselaer the arch again divides for a short distance as in northern Ohio.

In 1922 Malott* called attention to the trend of the axis in Indiana and to the relation of the arch to the strata and to topographic forms.

These two axes, one in Indiana, the other mainly in Ohio, if followed southward are found to unite just south of Cincinnati into a single broad swell or geanticline, which attains its maximum altitude as a structure in Jessamine County, Kentucky, in what is called the Jessamine Dome.

Toward the south the anticline can be traced easily across Kentucky and Tennessee into northern Alabama. The structure flattens out about 75 miles southwest of the Alabama-Tennessee line and passes under Cretaceous sediments. Becker† suggests that the Mesozoic and Tertiary strata of the coastal plain south and westward from this place show a broad low fold which can be traced across Mississippi and Louisiana. This of course is much later than the Cincinnati Anticline in as much as the latter was uplifted, arched and base leveled before these more recent beds were laid down. Hence it would probably be wiser not to consider such a structure as a part of the Paleozoic Cincinnati Anticline at all.

Summing up then we have a great Y-shaped structure whose south pointing stem is at least 300 miles long, whose eastern arm is of equal length between the fork and Lambton, Ontario, and whose western arm sweeps in a broad curve toward Kankakee, Illinois, with a length of 225 miles from the fork.

The anticline must be thought of as a structure and not as a form. While strata are everywhere in it arched into a grand, broad, low fold, the land along the crest is no higher than in other parts, and often not so high by a few hundreds of feet as the *cuestas* of flanking harder layers outcropping parallel with the axis.

* Malott, Clyde A. Ind. Geol. & Nat. Hist. Pt. 2. p. 127f.

† Becker. oral communication at Cincinnati meeting Sec. E. A. A. A. S. Dec. 29, 1923.

THE SECTIONS.

In order to carry forward this study, a series of structure sections have been drawn crossing the Anticline at selected places. Each section is essentially at right angles to the axis where drawn, and all are drawn on the same scale. In order that the arching may be visible, the horizontal and vertical scales hold such relation to each other that the vertical is exaggerated eight times. This makes the structure seem higher than it is, and portrays the dips much steeper on the flanks than they really are. We have, from its discovery, been told that it is a broad low arch, dome, fold, or anticline, but if one examines these sections and recalls that the vertical has an exaggeration of eight, he will be more than ever convinced of the value of the adjectives broad and low.

Since the relief of the land is so slight and generally more closely related to streams and valleys than to the structure of the anticline, the surface of the land is usually represented by a straight level line. A few valleys show and are so designated. The total relief over the whole area except for a few knobs in eastern Kentucky and others in central Indiana, probably does not exceed 1000 feet and this is so slightly related to the structure that it has been omitted. In the original drawings the horizontal scale was 4 miles to the inch and the vertical one-half mile to the inch. In the reductions for publication both are greatly reduced, but the ratio has been preserved. All sections are drawn and reproduced on the same scale. The sections are about one degree of latitude or 70 miles apart. The southern (No. 1) is in Tennessee and approximately on parallel 36° N., though lying obliquely across it. No. 2 in southern Kentucky, makes a small angle with parallel 37° N.; Nos. 3, 4 and 5 are respectively, essentially upon the next three parallels, while Nos. 6 and 7 are balanced obliquely, but not quite symmetrically on parallel 41° N. No. 6 is from northern Ohio, and No. 7 from northern Indiana. The sections were drawn from the four state geologic maps; Indiana on a scale of 4 miles to the inch, Ohio and Tennessee 8 miles to the inch, and Kentucky 12 miles to the inch. A contour map could be drawn on the Trenton if we had enough data. Well logs furnish excellent material if properly kept, and in most of Indiana and northern Ohio they are sufficient, but in other parts not yet available.

INTERPRETATION OF THE SECTIONS.

Section No. 1. Nashville Dome on the Anticline (Nashville Basin topographically) and this section cuts obliquely across it, N. W.-S. E. The anticline is here 120 miles across and 3,600 feet high. East dips average about 55 feet in a mile and west dips 50 feet.

Section No. 2. Intersects a sag in the crest, between the Nashville and Blue Grass basins or the Nashville and Jessamine domes. The structure is 140 miles wide and rises 2,100 feet on the west, but only 2,000 feet on the east. East dips are again steeper making this limb shorter. East dips average about 42 feet, west dips about 22 feet to the mile.

Section No. 3. Jessamine Dome. Width about 250 miles. Drillings show the Trenton limestone at Owensboro, near the west end of the section 3,500 feet below sea-level, and at eastern end of our section, about 3,300 feet below sea-level. Erosion has revealed the Trenton on the axis near Lexington with an altitude of 1,000 feet above sea level. Thus the structure along this line is 4,400 feet high. East dips are again much the steeper, averaging about 43 feet, and west dips about 31 feet.

Section No. 4. Crosses three states. About 35 miles in the central part is in Kentucky, while the eastern end is in Ohio and the western in Indiana. The structure here has a width of 215 miles and already shows the crest divided into two small swells, one east of Cincinnati and one west, with a sag of nearly 100 feet between them. Trenton rises in each crest to 50 or more feet above the river, showing at Patriot, Indiana, and Point Pleasant, in Ohio. The altitude attained here is essentially 3,000 feet, with dips a little stronger on the east side.

Section No. 5, A. & B. This section is divided into two parts at the Ohio-Indiana line, because it is so much longer than the others. It shows two axes clearly, one 30 miles east of the state boundary, and the other about 45 miles west. The sag between them is still very slight. The Ohio crest is 3,600 feet above the base of the eastern limb and the Wabash crest is about 2,600 feet above the western limb.

Section No. 6. Findlay dome on the east branch. The width here is 120 miles and the crest rises 2,800 feet above

the eastern limb and 1,300 feet, much more gently, above its western limb.

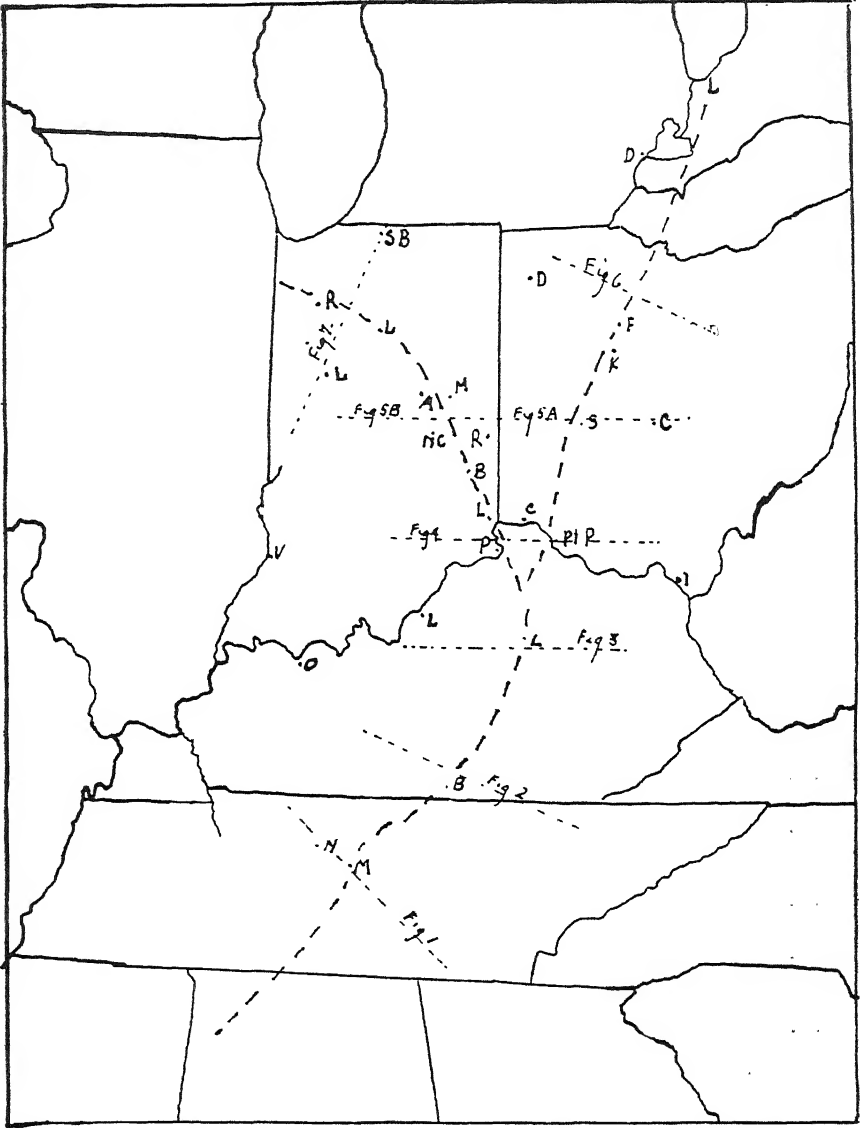
Section No. 7. Rensselaer dome on Wabash Arch. Section from South Bend, Ind., S. W. near Rensselaer, Remington, LaFayette and Rockville. The width is 150 miles at least and the altitude 1,600 feet, the least found anywhere.

THE UNEVEN TOPPED CRESTS.

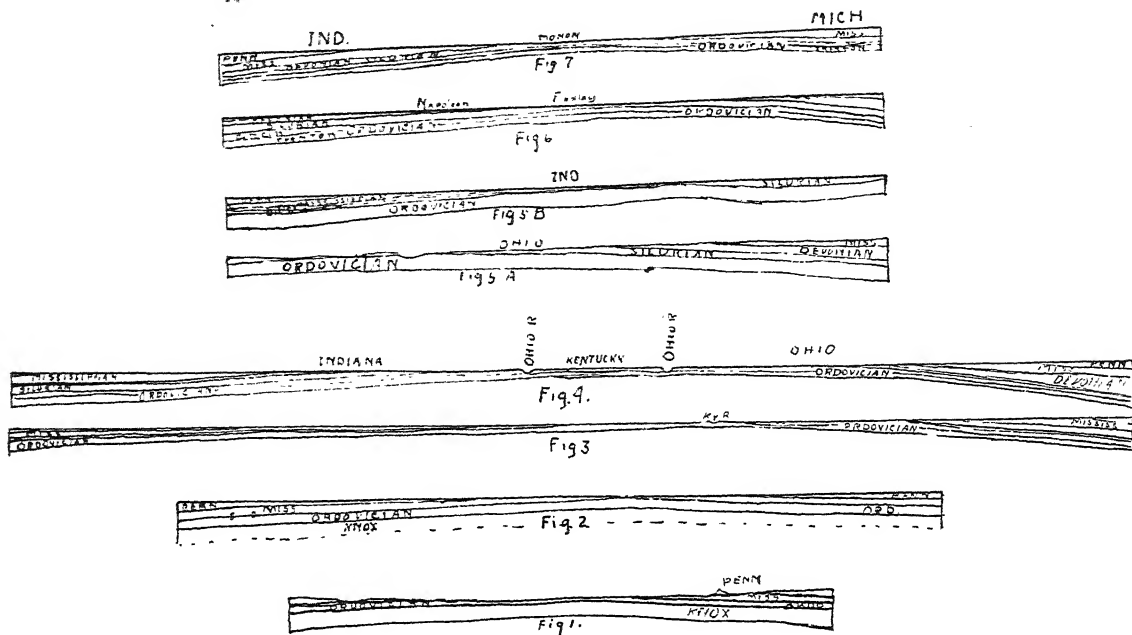
Another item of interest is the character of the crests of the Anticline. Beginning in the south and following the top of the Trenton limestone the figures may be given.

Murfreesboro, Tenn.....	950 ±	feet above sea level.				
Burkesville, Ky.....	250	"	"	"	"	"
Lexington, Ky.....	1000	"	"	"	"	"
Patriot, Ky.....	500 ±	"	"	"	"	"
Lawrenceburg, Ind.....	158	"	"	"	"	"
Brookville, Ind.....	174	"	"	"	"	"
Connersville, Ind.....	117	"	"	"	"	"
Anderson, Ind.....	66	"	"	"	"	"
Logansport, Ind.....	334	"	below	"	"	"
Rensselaer, Ind.....	158	"	"	"	"	"
Point Pleasant, O.....	500 ±	"	above	"	"	"
Springfield, O.....	450	"	below	"	"	"
Kenton, O.....	500	"	"	"	"	"
Findlay, O.....	340	"	"	"	"	"
Fostoria, O.....	600	"	"	"	"	"
Still lower under Lake Erie.						

Thus the crests are shown to be quite uneven topped, varying from 1,000— feet below sea level under western Lake Erie to 1,000 feet above near Lexington, Kentucky, and changing dip frequently along the axis. Dips along the axes however must be exceedingly small even compared with those on the flanks.



The group of states in which the Cincinnati Geanticline occurs. Heavy dashes show course of the main axes with branches; light dash lines show approximately the location of the seven sections. Dots with initial letters locate approximately most of the cities mentioned in the text.



- Fig. 1. Section in Tennessee basin with Murfreesboro nearly on the axis. Lower Ordovician corresponds roughly with lower Trenton of sections farther north.
- Fig. 2. Structure section in southern Kentucky with Burkesville nearly on the axis. Silurian and Devonian very thin.
- Fig. 3. Section through the Jessamine dome central Kentucky with Lexington near the axial line. The highest part of the anticline.
- Fig. 4. Structure section along 39° N. parallel. The first section to show the two crests. Trenton is high enough to show in Ohio River on each crest but not high enough to show along river between crests.
- Fig. 5. Divided into two parts, A in Ohio, B in Indiana. Two crests here 75 miles apart show clearly, one in Indiana, the other in Ohio.
- Fig. 6. Structure section without all the detail across arch in northern Ohio. The three minor folds near the crest are too small to show on a section on this scale.
- Fig. 7. Section nearly N-S in northern Indiana bearing same relation to Wabash Arch that No. 6 does to eastern branch. No. 6 and 7 are not continuous as No. 5A and 5B are. See Map.

THE OHIO JOURNAL OF SCIENCE

VOL. XXIV

JULY, 1924

No. 4

THE VASCULAR ANATOMY OF CALAMOVILFA LONGIFOLIA.*

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The present study of the anatomy of *Calamovilfa* was undertaken first because of the great difference observed between the mature vascular bundle of the rhizome and of the aerial stem. Both transverse and longitudinal sections were made of the rhizome and the writer was unable to find spiral tracheæ, although they occur in the aerial stem just as they occur in the other grasses. The investigation which followed then resolved itself into a study of the vascular strands: (1) the difference in the vascular structure of the aerial and subterranean stems, (2) the origin, development, and final organization of the vascular bundle of the stems, and (3) the development of the thickenings of the cell walls of the xylem vessels.

When one goes into the literature for a discussion of the above points there is an absence of definite data. Almost all the texts and reference books deal with the mature structures without taking up their origin and development. The figures that are used are mainly those of *Zea*, and only occasionally is some other grass figured. But though the vascular bundles of the aerial parts of grasses have many similarities, they are not all like corn and they are not all arranged in the stem, as they are in corn. It is possible because of these variations among the grass tribes to identify many genera and even species by their vascular anatomy. Schwendener, Duval-Jouve, Holm, Beal, Pammel, and others have studied the vegetative structures for the purpose of identification; and most of the anatomical studies have been of this type. For these studies in most

* Offered as partial requirement for the degree of Doctor of Philosophy at the University of Chicago.

instances the aerial parts were used. But in the grasses the stems vary in the composition of the mature vascular strand and in the arrangement of the vascular bundles, so that not only may the aerial stems of different species be dissimilar, but furthermore, (1) the underground stems of species are different and may form a basis for identification and (2) the aerial and underground stems of the same species are different from each other.

The writer has been unable to find papers which discuss the variation in the vascular anatomy between the rhizome and aerial stem of the same plant, or any discussing the origin and development of the vascular strands of the grasses.

THE RHIZOME.

The internode of the rhizome of *Calamovilfa* is very little elongated. There are few cells of the rhizome which are not lignified. All of the cells of the vascular bundle are thick walled and lignified, even those of the phloem (Fig. 1), although microchemical tests show that the cells of the phloem are not as highly lignified as those of the xylem and pericycle. The reduced leaves, merely scales, are also highly lignified and cutinized. The vascular bundle in the rhizome consists of the phloem with its sieve tubes and companion cells, protoxylem tracheids, and two to four large metaxylem tracheæ. It is without protoxylem annular or spiral tracheæ (Fig. 1), except in an occasional internode which has elongated or in a leaf trace. Instead, the protoxylem cells are thick walled, angular tracheids, and the pericycle is of thick walled, angular cells several layers wide. It forms a continuous band about the stele and the cortex on the inner side. The endodermis is not always well defined.

THE AERIAL STEM.

The aerial stem of *Calamovilfa* shows no differentiation of cortex, for the vascular strands are scattered through the stem around a central pith. Each bundle is surrounded by a thick walled pericycle of several cell layers, and the phloem is made up of large, thin walled sieve tubes with companion cells usually irregularly placed, although they are sometimes quite regular. There are usually two large metaxylem pitted vessels,

and from one to five annular and spiral vessels of the protoxylem surrounded by a few parenchyma cells, (Fig. 2).

The internode is said to develop basipetally. The writer has been unable to demonstrate any definite region of dividing cells at the base of the internode. The elongation in *Calamovilfa* occurs evidently from a diffuse region there which does not continue as cambium activity does, but is of limited development. Lignification begins at the top of the internode and progresses down the stem. The lignification of the base of the internode is the limit of the elongation phase of its development.

THE DEVELOPMENT OF THE INDIVIDUAL VASCULAR BUNDLE.

The desmogen strand is recognized first in the leaf primordium in both longitudinal and transverse sections. It begins with a single cell (Fig. 3), found and recognized with difficulty, that divides into two cells which are readily distinguished, (Fig. 4). Each of these cells divides longitudinally forming four cells (Fig. 5), and from here on the divisions are irregular. The cells of this strand press against the cells surrounding them and cause them to be elongated at right angles to the axis of growth (Fig. 6). This produces an appearance, which later disappears, of a sheath around the demogen strand.

When the strand reaches the condition shown in Figure 7, some of the cell walls both on the inner and outer edge of the strand may begin to thicken, but if elongation is rapid the thickening on the outer edge of the strand does not begin until after the metaxylem cells are differentiated. These outer cells, whose walls become thickened, are pericycle cells.

1. *The Development of the Vascular Bundles of the Aerial System.*

The cells which become thickened on the side of the strand toward the center of the stem are the annular and spiral tracheæ of the protoxylem. From one to five of these are differentiated. The mature condition is usually as follows: The first vessel is an annular one with the rings closer together than the first, or a spiral vessel very much stretched out. The succeeding ones formed centrifugally are spirals less and less elongated,

and the youngest either has the tightest spiral or may be a reticulate vessel. Figures showing this are to be found in a number of text and reference works. Metaxylem vessels (pitted vessels when mature) appear after this; the phloem is differentiated about the same time. The metaxylem vessels are formed from the cells at the periphery of the strand (Fig. 8) in the inner half of the bundle, and the phloem begins to develop from the outer portion of the outer half of the bundle and develops centripetally.

At the outer edge of the strand the walls of the pericycle cells begin to thicken and lignification of the bundle begins. This continues until only the phloem cells and a few cells about the annular and spiral vessels remain as thin walled cells.

The protoxylem develops centrifugally, and the phloem develops centripetally for a time; then the cells of the phloem enlarge and in doing so press against the cells between them and the protoxylem so that these cells are flattened to appear as a cambium region. Chrysler has reported cambial activity in the grass bundle, but in *Calamovilfa* although the mature bundle of the aerial parts appears to have a cambium, it certainly does not, for the condition shown in Figure 9 is brought about in the manner described above. The divisions of the cells of the strand, before the xylem and phloem are differentiated, takes place throughout the whole strand as is shown by the accompanying figure (Fig. 10). Consequently the cells may continue to divide between the xylem and phloem in the region just above the nodes (Chrysler) which is the last to be completely lignified, and the pressure of the developing xylem and phloem causes the cells to take on the appearance of a cambium.

2. *The Development of the Vascular Bundles Without Annular and Spiral Vessels.*

The bundle (Fig. 1) found in the slow growing rhizome develops in a different manner. The desmogen strand develops just as in the bundle described above until the strand is made up of from twenty to fifty cells. Then there appear usually two (at times one to four) large cells which form the large pitted vessels of the bundle (Fig. 11). The cell walls of the pericycle at the outer edge of the bundle begin to thicken and the cells of the protoxylem become lignified, but no annular

or spiral vessels are differentiated (except occasionally one and exceptionally two small ones) and all of the protoxylem cells are tracheids. The lignification, which started with the thickening of the cell walls of the pericycle and protoxylem, now continues until all of the cells of the bundle are thick walled and lignified (Fig. 1).

THE AMPHIVASAL BUNDLE.

The amphivasal bundle (Figs. 12 and 13) which one finds in the nodes and rhizome is brought about by the laying down of two vascular strands together which diverge and continue each as single strands. Sometimes the protoxylem vessels are not laid down, but usually in the aerial stem they are. Figure 12 shows the amphivasal bundle without annular or spiral vessels and Figure 13 shows an amphivasal bundle with a protoxylem spiral vessel. Chrysler has studied this condition in his paper on "The Nodes of Grasses" and states that the amphivasal bundle of the nodes is the fusion of two bundles and that in the basal portion of the plant this may continue through the internode. He also points out that the amphivasal bundle occurs more frequently in the rhizome and lower nodes of the plant than in the aerial nodes. This was found by the writer to be true in *Calamovilfa*. In *Zizania*, Chrysler finds that the amphivasal condition is most common where the nodes are crowded and that the same thing is true in the reproductive branch of corn, where the nodes are also crowded. Since the amphivasal bundle is so closely associated with the amount of elongation and the separation of the vascular strands, it is evident that here may be a means of studying the scattered vascular bundle that will lead to a better understanding of this condition in monocotyledons. That these structures will fit into the ordinary phylogenetic classification is not at all assured, although considered with other characters they may straighten up the relationships of the tribes and genera. Dr. Land, in his lectures, points out the great influence of the pericycle in the breaking up of the stele as the cambium activity becomes less pronounced. There is no doubt that a study of the pericycle and its development as well as a study of the endodermis will be of value for further investigations of the grasses and their inter-relationships.

THE MARKINGS OF THE XYLEM VESSELS.

According to Haberlandt there are five types of mature tracheæ in the xylem: annular, spiral, sclariform, reticulate, and pitted. All of these but the sclariform are found in *Calamovilfa*. As to the cause of the formation of these varying types, Haberlandt, Jeffrey, and others call attention to the fact that the annular and spiral vessels are related to the elongation of the stem or root, but they do not impress upon the reader the fact that annular and spiral thickenings are the direct result of elongation. Some writers even give the idea to their readers that they are annular and spiral to permit elongation rather than that they are the result of elongation.

In the rapidly growing aerial stem the first vessel to be laid down is usually observed to be either annular or spiral, succeeding vessels are closer spirals, and the last formed are reticulate or pitted. The writer finds that the type of vessels found in the mature condition varies with the amount of elongation, while the deposition of material forming the wall thickenings is going on. In very slow-growing stem tips no spirals are found, except occasionally a very tight one and occasionally an annular vessel. In elongating tips annular and spiral vessels of varying degrees are found in the protoxylem. The metaxylem tracheæ, laid down when elongation has practically ceased, are pitted vessels, or may be slightly reticulate.

In the rhizome with very short internodes the annular tracheæ are found occasionally, but few and scattered. These are the only protoxylem vessels found when any are found at all. In fast growing regions of the plant there are as many as five protoxylem annular and spiral vessels in the vascular bundles. In the internodes which are most elongated the elongation may be so great that the annular vessels are actually ruptured and even the surrounding parenchyma cells may be torn so that one finds the thickenings attached along the sides of a cavity. This is figured by Strasburger (page 122), and the cavity is readily demonstrated in corn and other grasses with a rapid development of aerial parts.

The above observation leads to a more careful study of the beginnings of these thickenings. Elongation occurs before these thickenings are lignified, and the thickened portion of the

wall must be, therefore, in a more or less plastic state. A careful examination of the longitudinal sections of the desmogen strands showed that the first thickening is laid down in the pitted form, (Fig. 14). Still younger cells show a vacuolation of the cytoplasm, (Fig. 15), which causes it to line the wall in the same pattern as shown by the first wall thickenings. Apparently then, division and enlargement of the surrounding cells (Fig. 16) tears apart this wall thickening (Fig. 14) and the cell becomes annular, spiral or reticulate, depending upon the amount of stretching. If elongation has ceased, as it has when the thickenings of the metaxylem vessels occur, the wall remains in a pitted condition. In text figures one usually sees these vessels with the spirals and annular rings very regular. This is true to a remarkable degree; but there are many exceptions to this, for irregularity is common.

Thus it is shown that the types of tracheæ vary with the amount of elongation, maximum stretching causing the formation of the annular vessel, decreasing degrees of elongation causing spirals, reticulate, and finally pitted vessels, in the order named. This accounts for the fact that one does not find annular or spiral vessels in secondary wood, where sclariform, reticulate and pitted vessels occur.

It is common knowledge that plant structures vary when under different environmental conditions and it is evident from this study that the vascular structures are possibly not as static as they have been regarded, since the form of the protoxylem tracheæ, as well as the number of tracheæ, varies with the amount of elongation of the internode.

The physiology of the deposition of the thickenings of the xylem vessels is an open question. It may be that subsequent observations of anatomical variations of plants in extreme situations may throw some light upon the reasons for the thickening of the walls laid down in specific cells. It is known that less lignification occurs in hydrophytic than in xerophytic habitats, but this is a secondary thing, for, in *Calamovilfa* at least, lignification occurs after considerable thickening of the cell wall has taken place.

The failure of certain cells to divide in one plane and the ability to divide in another is the thing that leads to the development of the xylem vessels. The reason underlying the failure

of the division at right angles to the main axis of the region of growth can at present be only a conjecture. (Dr. Land).

That the continued division and enlargement of the surrounding cells functions in the elongation of the protoxylem cells was called to our attention by Dr. Land from his work, as yet unpublished, on the origin of conductive strands. As soon as the division of the cells surrounding the xylem vessels ceases there are no more spiral vessels formed and all of the metaxylem vessels remain in the pitted condition.

The writer is indebted to Dr. W. J. G. Land for his advice and constructive criticisms, to Dr. E. N. Transeau for securing the equipment necessary to make these studies, and to the members of the staffs of both the University of Chicago and The Ohio State University for their help given unstintingly whenever it was asked.

SUMMARY.

1. The first appearance of the vascular strands of *Calamovilfa* is the leaf primordia.

2. The vascular strand starts with a single cell.

3. In the elongating parts the order of development is as follows: Annular and spiral protoxylem elements, differentiation of phloem and metaxylem at about the same time, and finally pericycle.

4. In the rhizome the vascular strand does not develop the annular and spiral protoxylem elements because of the failure of the elongation of the internode.

5. The amphivasal bundle of the nodes is brought about by the laying down of two bundles together which later diverge as simple strands.

6. There is no cambial activity in the vascular bundle of *Calamovilfa*.

7. A definite layer of dividing cells has not been found at the base of the internodes, but instead elongation occurs from a diffuse region of dividing cells.

8. The amount of elongation determines whether the tracheæ are annular, spiral, reticulate or pitted vessels.

9. The first thickening of all types of the tracheæ is pitted, and the walls are then stretched out by the division and enlargement of the surrounding cells so that they assume their mature form.

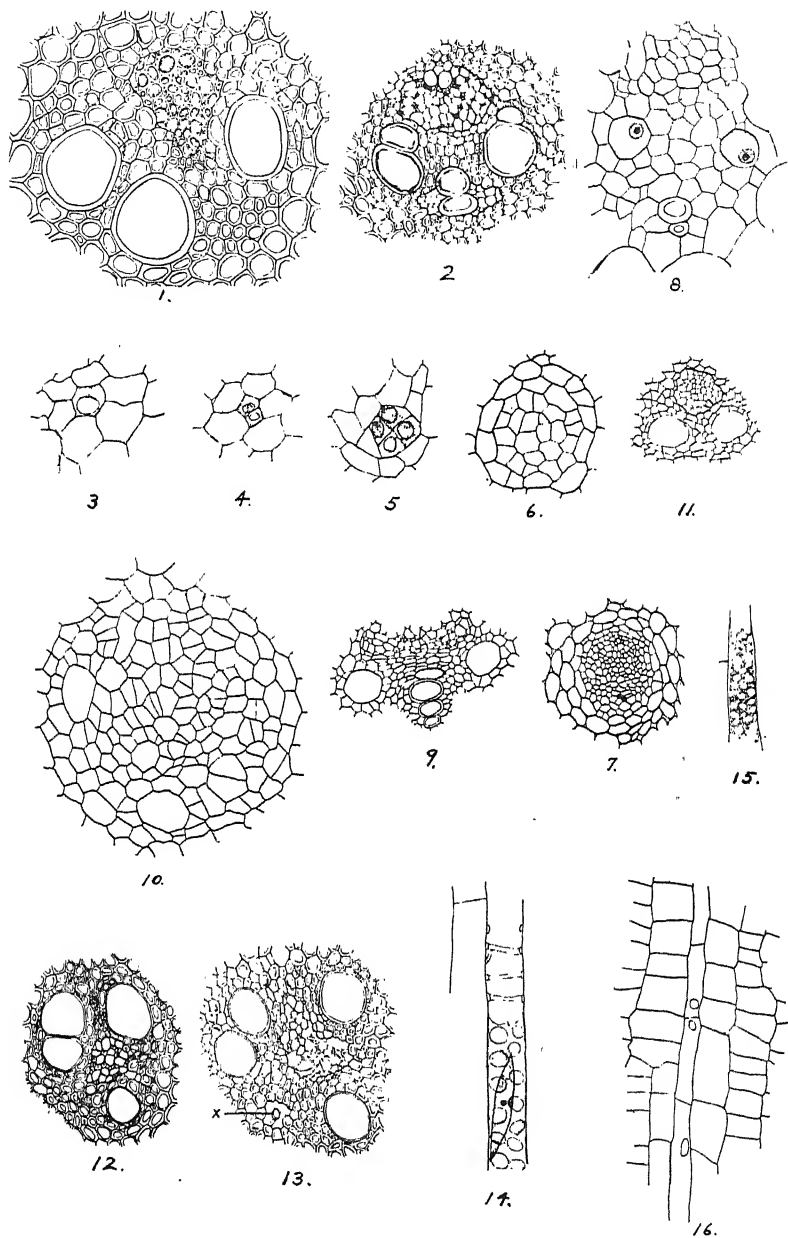
10. The original pitted thickening evidently arises by the vacuolation of the cytoplasm, this thickening being laid down by the thicker portions of the cytoplasm.

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EXPLANATION OF FIGURES.

- Fig. 1. Vascular bundle of rhizome, no protoxylem vessels, phloem lignified.
- Fig. 2. Vascular bundle of aerial stem, protoxylem vessels, (P).
- Figs. 3, 4 and 5. Development of desmogen strand from single cell to four-celled stage.
- Fig. 6. Desmogen strand showing appearance of sheath which disappears.
- Fig. 7. Young vascular bundle showing beginning of lignification. The lower thickened cells are protoxylem vessels, the upper the first cells of the pericycle to be lignified.
- Fig. 8. Young vascular bundle of aerial stem showing two protoxylem vessels and the beginning of the differentiation of metaxylem vessels and the phloem.
- Fig. 9. Cross section of vascular bundle just above the node of aerial stem, showing four protoxylem vessels (one not showing thickening), and semblance of cambium.
- Fig. 10. Desmogen strand showing the irregular division of cells throughout the strand.
- Fig. 11. Young bundle of rhizome without protoxylem vessels, but showing the beginning of the differentiation of metaxylem vessels and phloem.
- Fig. 12. Amphivasal bundle without protoxylem vessels.
- Fig. 13. Amphivasal bundle showing a protoxylem spiral vessel, (X).
- Fig. 14. A protoxylem cell showing the original pitted thickenings and spiral thickening in the same cell. The nucleus often remains after the cytoplasm disappears.
- Fig. 15. Protoxylem cell showing characteristic vacuolation of the cytoplasm.
- Fig. 16. Longitudinal section showing original cell of desmogen strand and divisions of surrounding cells which on enlargement stretch the cells in line with (X).



SOME NEW FORMS OF SPIROGYRA AND OEDOGONIUM*

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In collections of algæ from northwestern Iowa during† the summer of 1923 and from Ohio during the past four years, there have appeared some forms of *Spirogyra* and *Oedogonium* not previously described. In each of the following descriptions a Latin as well as an English diagnosis is given, supplemented by camera lucida drawings. In addition, notes are given on dates and places of collection and on relationships of each form of algæ described. There is appended a short discussion on the importance of knowing the manner of growth of groups of algæ, like the *Oedogoniaceæ*, if the collector desires to make a complete survey of any algal habitat.

The thanks of the writer are due Professor R. B. Wylie for the opportunity of collecting algæ in Iowa, and to Professor E. N. Transeau for critical suggestions given throughout the study of these new forms.

Spirogyra echinata nov. sp.

Cellulis vegetativis $88-96\mu$ latis, diametro 1-2-plo longioribus, dissepimentis planis; chromatophoris 4-7, anfractibus .5-1.5; vellulis fructiferis abbreviatis, et uno latere (in quo conjugatio sequitur) inflatis; zygosporis ovoideis, maturitate bruneis, crass. $68-85\mu$, diam. $76-120\mu$, mesosporio echinato.

Vegetative cells $88-96\mu \times 84-160\mu$, with plane end walls; 4-7 chromatophores making .5 to 1.5 turns; fertile cells shortened and inflated on the conjugating side; zygosporis ovoid, $68-85\mu \times 76-120\mu$, often placed transverse to the filament; median spore wall echinate, brown.

This species has an appearance, in general, similar to that of *Spirogyra reinhardii* Chmiel. and of *S. diluta* Wood. From the former it differs in dimensions and number of chromato-

*Papers from the Department of Botany, The Ohio State University, No. 148.

†The writer, upon the invitation of Professor R. B. Wylie, Head of the Department of Botany, The Iowa State University, spent the summer of 1923 at the Iowa Lakeside Laboratory, near Milford, Iowa. Several hundred collections of algae were made in the vicinity of the Laboratory. A systematic account of all the filamentous algae found in these collections is in progress.

phores. From both it differs markedly in having the middle wall of the zygospore very prominently echinate, the length of the echinate protuberances ranging from 6 to 9 μ . This alga was collected from a cut-off of the Little Sioux River near Montgomery, Iowa, July 17, 1923. Type in Iowa collections herb. L. H. T. Collection No. 121. Plate I, Fig. 1.

Spirogyra pellucida Kuetz. var. *minor* nov. var.

Cellulis vegetativis 30–36 μ latis, diametro 2–3-plo longioribus; zygosporis, crass. 40–56 μ , diam. 50–64 μ ; ceterum ut in typo.

Vegetative cells 30–36 μ x 73–100 μ ; zygospores 40–56 μ in thickness, 50–64 μ in diameter; otherwise as in the type.

This variety is easily distinguished from the type by its smaller dimensions throughout, particularly of the zygospores. *Spirogyra pellucida* Kuetz. apparently has not so far been recorded from America. The variety was collected by Mr. B. S. Meyer of the Department of Botany, the Ohio State University, in Baumgardner's Pond near Columbus, Ohio, May 3, 1923. Type in L. H. T. collections No. 354. Plate I, Fig. 2.

Oedogonium iowense nov. sp.

Oedogonium dioicum, macrandrium; oogoniis singulis vel binis, globosis vel ellipsoideo-globosis, operculo apertis, circumscissione superiore; oosporis eadem forma ac oogoniis, oogonia complentibus vel non complentibus, membrana lævi; antheridiis ad 25-cellularibus; spermatozoidis binis, divisione horizontali ortis; cellula fili, basali forma, ut vulgo, elongata;

crassit. cell. veget.....	10–16 μ ;	altit.	44–100 μ ;
“ oogon.....	52–60 μ ;	“	60–80 μ ;
“ oospor.....	45–56 μ ;	“	50–64 μ ;
“ cell. antherid.....	10–12 μ ;	“	10–20 μ ;
“ cell. basal.....	16–24 μ ;	“	60–80 μ .

Dioecious, macrandrous; oogonia single or in groups of two, globose or ellipsoid-globose, operculate, division superior; oospores of the same form as the oogonia which they completely fill or not, membrane smooth; antheridia 1–25 celled, sperms two, division horizontal; basal cells of filament commonly elongated;

Diam. veg. cells.....	10–16 μ ;	length	44–100 μ ;
“ oogonia.....	52–60 μ ;	“	60–80 μ ;
“ oospores.....	45–56 μ ;	“	50–64 μ ;
“ antheridial cells.....	10–12 μ ;	“	10–20 μ ;
“ basal cells.....	16–24 μ ;	“	60–80 μ .

This species bears some resemblance to *Oe. welwitschii* West, from which it differs in having smaller vegetative cells and larger oogonia. It differs from *Oe. pringsheimii* Cram.; Wittr. in having larger oogonia and oospores. The fact that the fruiting cells have a diameter of 3–6 times that of the vegetative cells gives this form a distinct place among the globose operculate species of Oedogonium. It was collected during July and August, 1923, in sloughs and bayous of West Lake Okoboji, Iowa. Type in Iowa collections herb. L. H. T. Collections No. 161, 194, 213. Plate III, Figs. 1–3.

Oedogonium latiusculum nov. sp.

Oedogonium dioicum, macrandrium; oogoniis singulis vel binis, globosis vel ellipsoideo-globosis, operculo apertis, circumscissione mediana, latissima; oosporis eadem forma ac oogoniis, oogonia complentibus vel fere complentibus, membrana lævi; plantis masculis paullulum crassioribus quam femineis; antheridiis unicellularibus, saepe cum cellulis vegetativis alternis; spermatozoidis singulis; cellulis vegetativis evidenter capitellatis; cellula fili basali subhemisphærica, non elongata; filis haud raro calce incrustatis;

crassit. cell. veg. fem.....	10–18 μ ;	altit. 16–40 μ ;
“ cell. veget. masc.....	14–20 μ ;	“ 16–40 μ ;
“ oogon.....	32–36 μ ;	“ 32–40 μ ;
“ oospor.....	28–32 μ ;	“ 28–34 μ ;
“ cell. antherid.....	14–18 μ ;	“ 12–20 μ ;
“ cell. basal.....	16–24 μ ;	“ 12–16 μ .

Oedogonium dioecious, macrandrous; oogonia single or in groups of two, globose to ellipsoid-globose; oogonium operculate, division median, very wide; oospores of the same form as the oogonia, which they very nearly or completely fill, wall smooth; male plants somewhat larger than the female; antheridia unicellular, usually separated by a single vegetative cell, sperm one; vegetative cells distinctly capitellate; basal cell of filament subhemispherical, not elongated; filaments not infrequently incrustated with lime;

diam. veg. cells, female.....	10–18 μ ;	length 16–40 μ ;
“ veg. cells, male.....	14–20 μ ;	“ 16–40 μ ;
“ oogonia.....	32–36 μ ;	“ 32–40 μ ;
“ oospores.....	28–32 μ ;	“ 28–34 μ ;
“ antheridial cells.....	14–18 μ ;	“ 12–20 μ ;
“ basal cells.....	16–24 μ ;	“ 12–16 μ .

This species is evidently near *Oe. pratense* Transeau, but differs in its much shorter and distinctly capitellate vegetative cells, in the shape of its basal cells, and in the differently shaped operculate oogonium with its wide opening. The dioecious habit

and the distinctly capitellate vegetative cells easily separate it from *Oe. acmandrium* Elfv. and from *Oe. psægmatorum* Nordst. From *Oe. capitellatum* Wittr. it is further distinguished by its larger dimensions throughout. It was collected in June, July, and August, 1923, in Miller's Bay of West Lake Okoboji, in the East Bay of Spirit Lake, in Clear Lake, and in Swan Lake, Iowa. Type in Iowa collections herb. L. H. T. Collections No. 7, 146, 168, 212. Plate III, Figs. 4-6.

Oedogonium infimum nov. sp.

Oedogonium dioicum, macrandrium; oogoniis singulis, globosis vel subglobosis (vel interdum parte basali paullo magis evoluta subpyriformi-globosis), operculo apertis, circumscissione infima; oosporis globosis vel subdepresso-globosis, oogonia fere complentibus, membrana lævi; plantis masculis paullo crassioribus quam femineis; antheridiis 1-10 cellularibus, spermatozoidis binis; cellulis vegetativis evidenter capitellatis; cellula fili basali subhemisphærica, non elongata; filis haud raro calce incrustatis;

crassit. cell. veget. fem.....	12-18 μ ;	altit. 60-140 μ ;
" cell. veget. masc.....	16-20 μ ;	" 60-140 μ ;
" oogon.....	40-48 μ ;	" 41-50 μ ;
" oospor.....	40-44 μ ;	" 38-42 μ ;
" cell. antherid.....	14-20 μ ;	" 8-12 μ ;
" cell. basal.....	30-42 μ ;	" 16-24 μ .

Oedogonium dioecious, macrandrous; oogonia single, globose or subglobose (or the basal part extended, appearing subpyriform-globose); operculate, division at the lowest extremity of the oogonium; oospores globose or subglobose, membrane smooth; male plants a little larger than the female; antheridia 1-10 celled, sperms two; vegetative cells distinctly capitellate; basal cell of filament subhemispherical, not elongated; filaments not infrequently incrustated with lime.

diam. veg. cells, female.....	12-18 μ ;	length 60-140 μ ;
" veg. cells, male.....	16-20 μ ;	" 60-140 μ ;
" oogonia.....	40-48 μ ;	" 41-50 μ ;
" oospores.....	40-44 μ ;	" 38-42 μ ;
" antheridial cells.....	14-20 μ ;	" 8-12 μ ;
" basal cells.....	30-42 μ ;	" 16-24 μ .

This species bears some resemblance to *Oe. inversum* Wittr. and the variety *subclusum* (Wittr.) Hirn. It differs from both in its larger dimensions and in having the male filaments larger than the female. The decidedly basal division of the operculate oogonium is its chief distinctive character. Hirn* in his

*Hirn, Karl E. Monographie und Iconographie der Oedogoniaceen. Helsingfors. 1900, p. 43.

tabular arrangement of the species of *Oedogonium* makes seven subdivisions of the globose, operculate forms, depending upon the position of the division of the oogonium. These subdivisions are: "Circumscissio: suprema, superior, supramediana, mediana, inframediana, inferior, infima." Hirn records no form of *Oedogonium* belonging to the group "Circumscissione infima." This, therefore, is apparently the first record of any species, either poriferous or operculate, belonging in that class; to designate such a decidedly basal opening the specific name *infimum* (L. *infimus*, lowest) is given. The outer spore wall, when not fully mature, sometimes appears slightly undulate, but this must not be taken to indicate an *Oedogonium* with rough-walled spores. So far this species has been recorded from Swan Lake and Clear Lake, Iowa, collected during July and August, 1923. Type in Iowa collections herb. L. H. T. Collections No. 146, 155, 231. Plate II, Figs. 6-9.

Oedogonium exspirale nov. sp.

Oedogonium dioicum, nannandrium, idioandrosporum; oogoniis singulis vel rarius binis, subglobosis vel oboviformi-globosis (rarius subhexagonis), poro mediano apertis; oosporis globosis vel subglobosis, oogonia fere complentibus, membrana duplici: episporio costis spiralter dispositis, costis spiralibus numero 5-8, utrinque in polo, in sectione horizontali, fere mediano, nunquam verticali sito conniventibus, endosporio lævi; cellulis suffultoribus tumidis; androsporangii 1-6 cellularibus; cellula fili basali forma, ut velgo, elongata; nannandribus paullulum curvatis, in cellulis suffultoribus sedentibus, antheridio exteriore, 1-3 cellulari;

crassit. cell. veget.....	8-12 μ ;	altit. 60-88 μ ;
" cell. suffult.....	16-28 μ ;	" 60-88 μ ;
" oogon.....	40-44 μ ;	" 44-48 μ ;
" oospor.....	32-38 μ ;	" 38-40 μ ;
" cell. andros.....	12-16 μ ;	" 14-20 μ ;
" stip. nannandr.....	14-16 μ ;	" 30-40 μ ;
" cell. antherid.....	8-12 μ ;	" 14-16 μ .

Oedogonium dioecious, nannandrous, idioandrosporous; oogonia single or rarely in groups of two, subglobose or oboviform-globose (rarely subhexagonal), pore median; oospores globose or subglobose, nearly filling the oogonia, membrane double, outer spore wall marked by 5-8 spiral ribs uniting at the poles, the polar axis always placed in a transverse position, never parallel with the filament, the inner spore wall smooth; suffultory cells swollen; androsporangia 1-6 celled; basal cells elongate; dwarf males a little curved, situated on the suffultory cells, with exterior antheridia 1-3 celled;

diam. veg. cells.....	8-12 μ ;	length	60-88 μ ;
" suffultory cells.....	16-28 μ ;	"	60-88 μ ;
" oogonia.....	40-44 μ ;	"	44-48 μ ;
" oospores.....	32-38 μ ;	"	38-40 μ ;
" androsporan. cells.....	12-16 μ ;	"	14-20 μ ;
" dwarf male stipe.....	14-16 μ ;	"	30-40 μ ;
" antheridial cells.....	8-12 μ ;	"	14-16 μ .

Forms of *Oedogonium* nearest this species are *Oe. illinoiense* Transeau and *Oe. spirale* Hirn. From both it differs in the considerably smaller dimensions of the vegetative and fruiting cells. It further differs from the former in being idioandrosporous. It is readily separated from *Oe. huntii* Wood by the median position of the pore of the oogonium and by its dimensions. The form was recorded from the East Bay of Spirit Lake and from a slough north of West Lake Okoboji, Iowa, during July and August, 1923. Type in Iowa collections herb. L. H. T. Collections No. 161, 168. Plate II, Figs. 1-3.

Oedogonium supremum nov. sp.

Oedogonium dioicum, nannandrium, idioandrosporum; oogoniis singulis vel rarius 2-4 continuis, globosis vel ellipsoideo-globosis, sæpe terminalis; operculo apertis, circumscissione surpema, operculo sæpe deciduo; oosporis eadem forma ac oogoniis, hæc plaen complementibus, membrana lævi; cellulis suffultoriis eadem forma ac cellulis ceteris; androsporangii 1-6 cellularibus; cellulis vegetativis evidenter capitellatis; cellula filii basali forma, ut vulgo, elongata; nannandribus late oboviformibus, unicellularibus, in oogonis sedentibus;

crassit. cell. veget.....	24-32 μ ;	altit.	60-132 μ ;
" oogon.....	66-78 μ ;	"	72-90 μ ;
" oospor.....	60-66 μ ;	"	66-84 μ ;
" cell. andros.....	26-28 μ ;	"	30-40 μ ;
" nannandr.....	20-24 μ ;	"	24-26 μ ;
" cell. basal.....	28-32 μ ;	"	90-110 μ .

Oedogonium dioecious, nannandrous, idioandrosporous; oogonia single or rarely in groups of 2-4, globose or ellipsoid-globose, often terminal, operculate, division at the upper extremity of the oogonium, lid often deciduous; oospores of the same form as the oogonia which they completely fill, membrane smooth; suffultory cells of the same form as the other vegetative cells; androsporangia 1-6 celled; vegetative cells distinctly capitellate; basal cell of the filament elongated; nannandrium broadly oboviform, unicellular, situated on the oogonia;

diam. veg. cells.....	24-32 μ ;	length	60-132 μ ;
" oogonia.....	66-78 μ ;	"	72-90 μ ;
" oospores.....	60-66 μ ;	"	66-84 μ ;
" androsporan. cells.....	26-28 μ ;	"	30-40 μ ;
" dwarf males.....	20-24 μ ;	"	24-26 μ ;
" basal cells.....	28-32 μ ;	"	90-110 μ .

This species is nearest *Oe. praticolum* Transeau and *Oe. obtruncatum* Wittr., from both of which it differs in having much larger dimensions and differently shaped oogonia and oospores. The terminal cells are not apiculate. It differs from *Oe. kitutae* West in being operculate, and in the general form of the vegetative and fruiting cells. Since this species is one of the few forms whose operculate division is at the upper extremity of the oogonium, the specific name *supremum* (L. *supremus*, highest) is applied. It was found in West Lake Okoboji, Iowa, during August, 1923. Type in Iowa collections herb. L. H. T. Collection No. 194. Plate I, Figs. 3 and 4; Plate II, Figs. 4 and 5.

Oedogonium grande Kuetz.; Wittr. var. *robustum* (Hirn) nov. comb.
Hirn: Monographie und Iconographie der Oedogoniaceen, p. 144, 1900.

Var. *omnibus partibus crassioribus*;

crassit. cell. veget. fem.....	32-46 μ ;	altit. 80-200 μ ;
" cell. veget. masc.....	32-42 μ ;	" 80-200 μ ;
" oogon.....	52-68 μ ;	" 75-90 μ ;
" oospor.....	50-64 μ ;	" 68-88 μ ;
" cell. antherid.....	30-36 μ ;	" 10-16 μ .

Somewhat larger than the type in all dimensions;

diam. veg. cells, female.....	32-46 μ ;	length 80-200 μ ;
" veg. cells, male.....	32-42 μ ;	" 80-200 μ ;
" oogonia.....	52-68 μ ;	" 75-90 μ ;
" oospores.....	50-64 μ ;	" 68-88 μ ;
" antheridial cells.....	30-36 μ ;	" 10-16 μ .

Although listed by Hirn as a robust form of *Oe. grande*, its very common occurrence in American material generally, either with the type or separate, seems to warrant a varietal rank. The American forms are considerably larger than the type. This variety along with the type is normally a summer annual, occasionally fruiting as early as June or as late as September. Plate III, Fig. 7.

Filaments of *Spirogyra* are usually found free-floating in quiet bodies of water, or remain stationary because they are associated, accidentally or otherwise, with other algæ or flowering plants that are attached to the substratum. It generally is true that one is likely to find a considerable mass of a species of *Spirogyra*, if collections are made in the proper season, instead of isolated individuals.

Species of *Oedogonium*, on the contrary, may be attached by holdfast cells during their entire vegetative and reproductive periods of growth. Some forms, such as *Oe. capilliforme* Kuetz.; Wittr., *Oe. crassiusculum idioandrosporum* Nordst. et Wittr., *Oe. grande* Kuetz.; Wittr., and *Oe. anomalum* Hirn, frequently form individual or collective masses of considerable size with holdfast cells difficult to find. Such species as *Oe. iowense*, *Oe. latiusculum*, *Oe. infimum*, *Oe. supremum*, and *Oe. exspirale* (described above), as well as many others, including *Oe. inversum* Wittr., *Oe. nanum* Wittr., and *Oe. praticolum* Transeau, are not known to form such masses. They occur as epiphytes on the leaves and stems of submerged higher plants and on species of *Cladophora*, *Pithophora*, and larger *Oedogoniums*. The number of such epiphytes upon their hosts is usually small and is further reduced pretty close to a minimum in the small sample that makes up the microscopic mount of the material. It is for the reason of this more or less solitary existence that species of *Oedogonium* are so often overlooked by collectors of algæ, not only in the field but also after they may be safely preserved in collections!

Many of the smaller species of *Oedogonium* are often so incrustated with such a heavy deposit of lime (mostly CaCO_3) that even generic identification is difficult. If filaments so incrustated are placed on a slide, a few drops of lactic acid added, and the whole gently heated, the entire incrustation is removed without injury to the cells or changes in their dimensions. In addition, the basal cells, often a species criterion, are made perfectly visible.

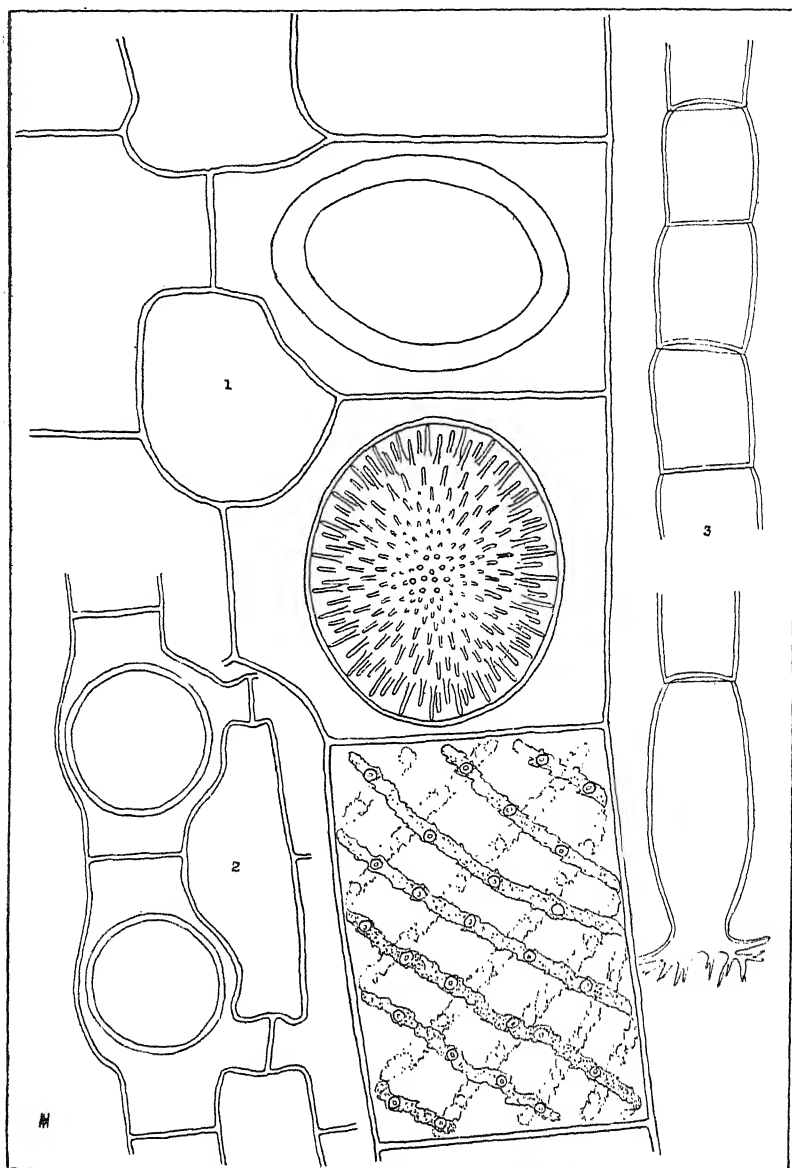
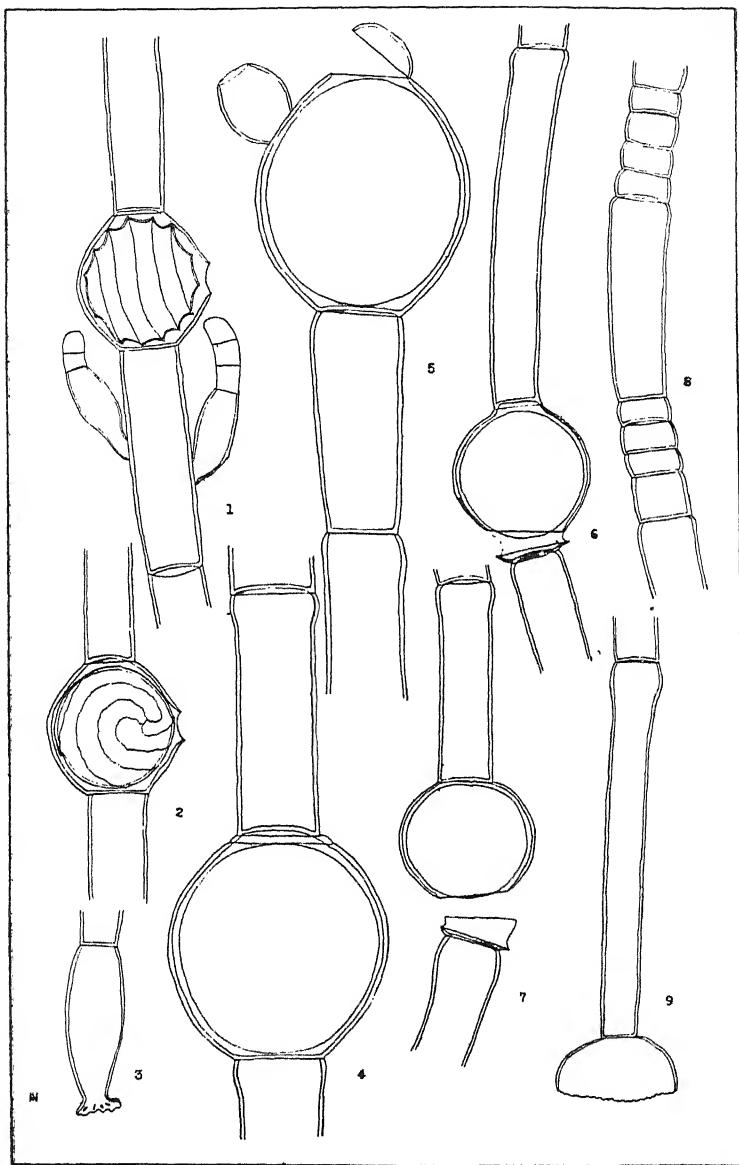
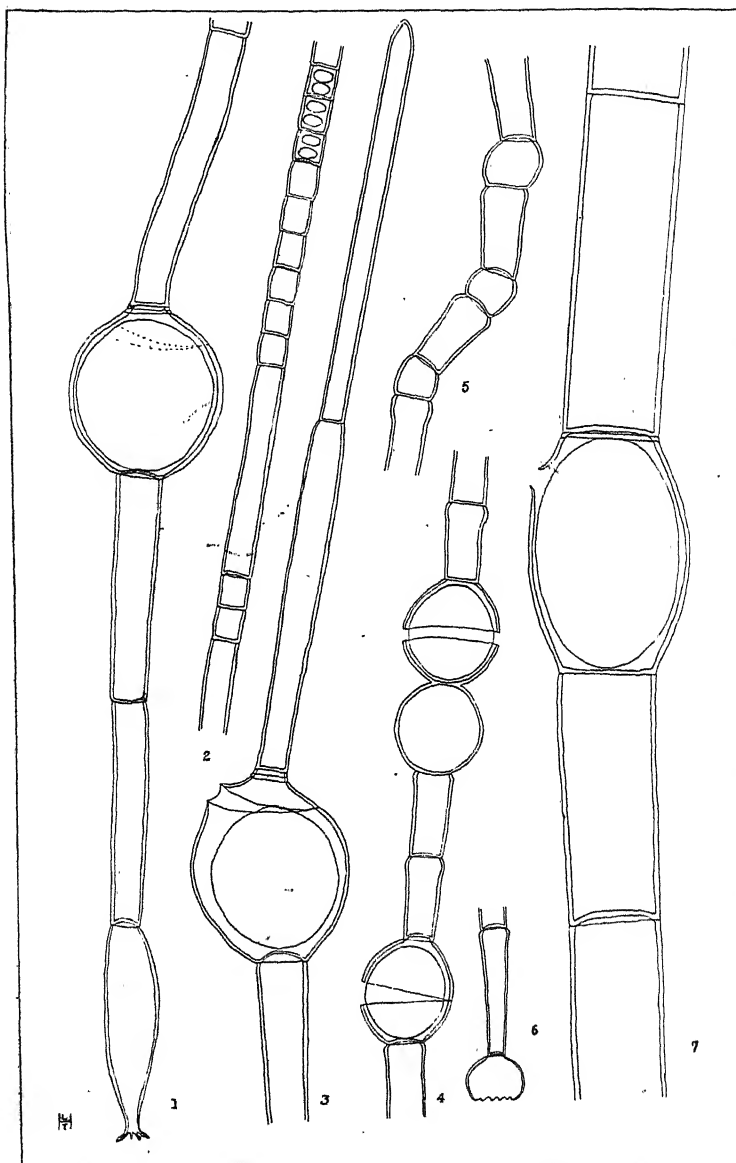


Fig. 1. *Spirogyra echinata*, showing chromatophores of one vegetative cell, a mature zygospore with echinate protuberances, and the variable position of the spore.
Fig. 2. *Spirogyra pellucida* var. *minor*.
Fig. 3. Androsporangial cells of *Oedogonium supremum*.
Fig. 4. Basal cell of filament of *Oedogonium supremum*.



Figs. 1-3. *Oedogonium exspirale*.
Figs. 4-5. *Oedogonium supremum*.
Figs. 6-9. *Oedogonium infimum*.



Figs. 1-3. *Oedogonium iowense*.

Figs. 4-6. *Oedogonium latiusculum*.

Fig. 7. *Oedogonium grande* var. *robustum*.

NEW PARASITIC HYMENOPTERA OF THE SUBFAMILY ANTEONINÆ (BETHYLIDÆ).

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During 1923, a number of dryinid wasps were bred from several species of *Cicadellidæ* and *Fulgoridæ* collected in Iowa. Upon examination, at least three species were found to be new and are described for the first time in this paper. One of these, namely, *Aphelopus bicolor*, had caused about ten per cent parasitism of its host, *Erythroneura trifasciata* Say. The larvæ of this species have also been collected in Ohio but were not reared through to the adult stage. *Aphelopus comesi* Fent. was also bred from *Erythroneura vulnerata* Fitch, collected at Spring Hill, Iowa. About half of the last named host species which were collected were parasitized.

Pseud ogonatopus iowensis n. sp.

The most striking characteristic of this species is the pale yellow tenth antennal joint, which contrasts sharply with the other dusky joints of the flagellum. Length, 2.81 mm. General color fuscopiceous. Eyes and vertex of head fuscous; frons and occiput, mandibles except teeth, clypeus and scape of antenna testaceous; tenth joint of antenna pale yellow; prothorax ferruginous with black on each side of the transverse emargination; thoracic constriction black, except ventral part and a narrow area down the center of the dorsum, which are testaceous; legs yellow to testaceous, except anterior femora, which are fuscous dorsally; propodeum piceous; abdomen fusco-piceous.

Head.—Vertex slightly concave, broader than long (19:12), surface closely and minutely punctate. Scape of antenna slightly more than twice as long and somewhat thicker than second joint; third about the same thickness as second and more than twice as long; fourth slightly more than half as long as third and somewhat thicker; fifth to eighth inclusive of nearly the same length and width, each being one-fourth shorter and slightly thicker than the fourth and slightly increasing in width towards the tip; ninth shorter than these; tenth less than twice length of ninth and of same thickness.

Thorax.—Prothorax shining with very fine microscopic punctation. Thoracic constriction slightly longer than wide (5:4), with surface minutely roughened, due to fine reticulation.

Propodeum.—Surface with dense punctation; anterior portion with irregular, coarse rugulosity; posterior third beginning just back of the

disc with a series of transverse rugose lines which extend down the sides. Type shows scattered fine white hairs present on this part.

Chela.—(Fig. 3). Median arm with a cluster of lamellæ at the tip and a row extending from a point near this nearly down to the articulation with the lateral arm, the lamellæ being somewhat farther separated from each other near this point. Lateral arm with six smaller, rather widely spaced lamellæ.

Described from one specimen bred from *Liburnia lutulenta* Van Duzee*, Ames, Iowa, July 21, 1923. Type in writer's collection.

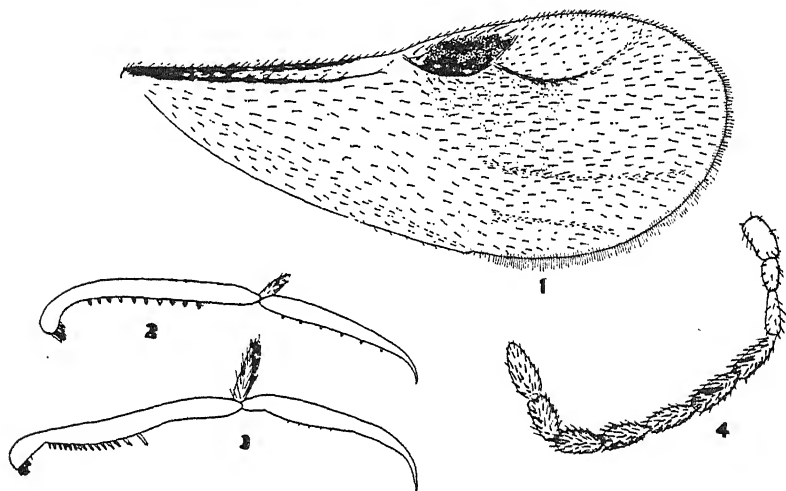


Fig. 1. Fore wing of *Aphelopus bicolor*.
Fig. 2. Chela of *Pseudogonatopus iowensis*.
Fig. 3. Chela of *Chalcogonatopus nigrus*.
Fig. 4. Antenna of *Aphelopus bicolor*.

Aphelopus bicolor n. sp.

A reddish brown species quite distinct from any others with which I am familiar. Length, 1.5–1.59 mm., alar expanse, 1.1–1.2 mm. Head testaceous except compound eyes, which are black, and teeth of mandibles, which are deep amber; first two antennal segments and basal part of third testaceous; rest of antennal segments brown. Mesonotum and scutellum testaceous; post-scutellum and basal portion of propodeum except extreme posterior margin, shining black; rest of propodeum testaceous; legs testaceous, except hind tibiæ and fifth tarsal joints, which are fuscous; fore wings with fuscous band extending below pterostigma and greater part of radius (Fig. 1); abdomen shining

* The host species from which these parasites were bred were kindly determined for the writer by Professor Herbert Osborn.

brown. Head and thorax with fine short pubescence; propodeum with very sparse, indistinct pubescence.

Head.—Broader than deep, (14:8); pattern a fine reticulation. Anterior ocellus slightly closer to the two lateral ones than these are from the hind margin of the head; compound eyes with sparse short, white pubescence. Clypeus arcuate; mandibles four-dentate, with three large teeth and one smaller inconspicuous one; maxillary palpi long and extending considerably beyond base of the head to the thorax, with four joints visible.

Antennæ of median length. First antennal joint slightly thicker and one-fourth longer than second; third of same length as first, somewhat more slender than second; fourth to sixth each one-fifth longer than third and of same thickness as second; seventh to ninth subequal, each being slightly shorter than sixth; tenth three-fifths longer than ninth; from the sixth to the ninth, each succeeding joint is slightly shorter and thicker than the preceding. (Fig. 4).

Thorax.—Mesonotum with same pattern as head; parapsidal furrows distinct, converging and extending about half way to caudal border of mesonotum; scutellum of same pattern as head and mesonotum; postscutellum and propodeum coarsely reticulately sculptured, the reticulations being large, with distinct raised lines. A distinct median smooth area is present on the dorsal posterior part of the propodeum.

Wings.—Fore wings in ratio of 30:13, hind wings, 22:6.

Abdomen.—Compressed laterally, sparsely pubescent.

Paratype. In this specimen the propodeum is entirely piceous on the dorsum, otherwise the coloration is the same.

Bred from *Erythroneura trifasciata* Say, Collected at Spring Hill, Iowa, October, 1922. Type in writer's collection.

Chalcogonatopus nigrus n. sp.

Length 2.448 mm. Black except antennæ, legs, face and a small area on the first abdominal segment, which are fuscous or testaceous. Antennæ fuscous except the first joint, which is testaceous; mandibles testaceous except the teeth; face testaceous just above the bases of the antennæ; compound eyes fuscous. Fore coxæ testaceous, except a fuscous area on the dorsal side extending two-thirds the distance of this joint from its base; fore trochanters testaceous; fore femora fuscous except distal parts at the union with the tibiæ, which are testaceous, somewhat darker dorsally; fore tibiæ fuscous except proximal part near the union with the femora, which are testaceous; fore metatarsi fuscous, rest of fore tarsi, including chelæ, testaceous; incrassate parts of the median and hind legs fuscous. The small tapering part of the propodeum near the petiole is testaceous, as well as a small area on dorsal part of the first abdominal segment just beyond the petiole.

Head.—Broader than long (18:10); slightly concave, showing under high power a very indistinct reticulation which is more distinct

posteriorly from the occipital region to just back of the median ocellus; two spur-like areas of this more distinct reticulation extend forward as far as the median ocellus, but a little to each side of it. Mandibles four-dentate; antennæ long; first joint twice the thickness of the rest, one-third longer than the second; third twice the length of the first, slightly more slender than the second; fourth slightly longer than the first or fifth, which are of the same length, and of the same thickness as the third; sixth, seventh, and eighth of equal length, each being one-fourth shorter than the fifth; ninth short, two-thirds the length of eighth; tenth twice the length of the ninth, same length as first.

Thorax.—The pronotum divided by an arcuate deeply impressed transverse line, the shorter, wider anterior portion being smooth and shining, the narrow elongated posterior division being finely reticulately sculptured. Thoracic constriction longer than wide (7:4) with several distinct longitudinal wrinkles or folds dorsally, extending throughout its length, except anteriorly, where the surface is smooth and polished.

Propodeum.—Propodeum with a distinct transverse rugulosity which also extends down the sides; disc with a fine reticulation. An indistinct, short, scattered pubescence is present.

Chela.—(Fig. 2). Median arm with a cluster of lamellæ at the tip, and a row of smaller ones extending from a point near the tip, half-way down to the articulation of this joint with the lateral arm, the last two lamellæ being longer than the rest.

Described from one specimen bred from *Scaphoideus* sp. probably *immistus* Say, July 8, 1923, collected by C. J. Drake. Type in writer's collection.

SOME OBSERVATIONS ON THE LIFE CYCLE AND HABITS OF DORYDIELLA FLORIDANA BAKER (HOMOPTERA-CICADELLIDÆ).

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While working with *Cicadellidæ* during the past few years, several interesting species have been found and studied. *Dorydiella floridana* is one which has been especially interesting to the writer because of its accidental discovery and in view of the fact that practically nothing was known concerning its habits. It was described by Baker in 1897 from material collected in Florida. During the past twenty-five years it has been taken occasionally in New Jersey, Tennessee, Massachusetts, Pennsylvania, Indiana, Illinois and South Dakota. Its range is therefore quite extensive, although it has been considered as a so-called rare insect and there are very few specimens even in specialists collections. During the summer of 1919 an ecologic study of the leafhoppers of Presque Isle, Pa., was undertaken and this species was collected in general sweeping near one of the numerous lagoons. When it was known that the insect occurred in this area, a detailed search was made to determine under what conditions and upon what plant the insect lived.

It was found to be living on *Scleria verticellata* in the *Eleocharis obtusa* association. Further observations showed that it may be found any place where it is sufficiently moist for the growth of this plant, but the optimum condition apparently for the insect, judging from relative numbers, is on the moist sandy soil within the lagoon basin, but far removed from the receding water. Undoubtedly the reason it has been collected so rarely is due to the fact that it feeds in both nymphal and adult stages on the succulent growth just above the surface of the ground and within the clump. Although only an occasional adult could be obtained by sweeping, several hundred specimens, both nymphs and adults, were obtained by picking apart clumps of *Scleria*. The nymphs were especially difficult to find at first because they were so well concealed between the leaves and so protectively colored. The brownish mottled

color, together with their elongate flattened shape, causes them to resemble so closely the dried blades of grass that their movements alone are responsible for their recognition. The movements of the nymphs especially, and to some extent those of the adults, are very sluggish and even when disturbed they will usually cling to some portion of the plant.

LIFE CYCLE NOTES.

Observations on the life cycle show that there is but one generation a year. The insect overwinters as an egg. These begin hatching in late May or early June, the first adults appearing about the middle of July. Although specimens in nymphal instars are found until September, all of these are late individuals of the first generation. Observations have been made only on the number of instars and the total length of time spent in the nymphal stage. No attempt has been made to obtain data on the length of time for the individual instars. The total length of time from egg to adult is about six weeks. There are five nymphal instars, three of which have been photographed and described here.

DESCRIPTION OF INSTARS.

Second Instar. (Figure 1).

Vertex long and flattened, apex blunt, spoon-like, slightly concave. Vertex longer than thorax, four times longer than pronotum, more than two-thirds as long as entire abdomen. Face with a very prominent keel extending from tip of vertex to clypeus. Sides of face deeply concave from edge of keel to edge of vertex. Length, 4 mm.

Color: Dirty white, irrorate with brown. Tip of vertex with a brownish cross, a rather broad median longitudinal stripe, and a short one next either eye, pale. Eyes red. Three longitudinal pale stripes, a continuation of those on vertex, extending across thorax and abdomen. Each abdominal segment excepting last with a conspicuous black spot either side just above rounded pleural portions. Face dark brown. Edge of keel, margin just below vertex and two oblique lines crossing face, pale. Legs irrorate with brown, venter pale yellow to reddish, a double median longitudinal line and side portions of plates brownish.

Posterior segment of abdomen cleft, forming two pointed projections.

Fourth Instar. (Figure 2).

Length 7 mm.

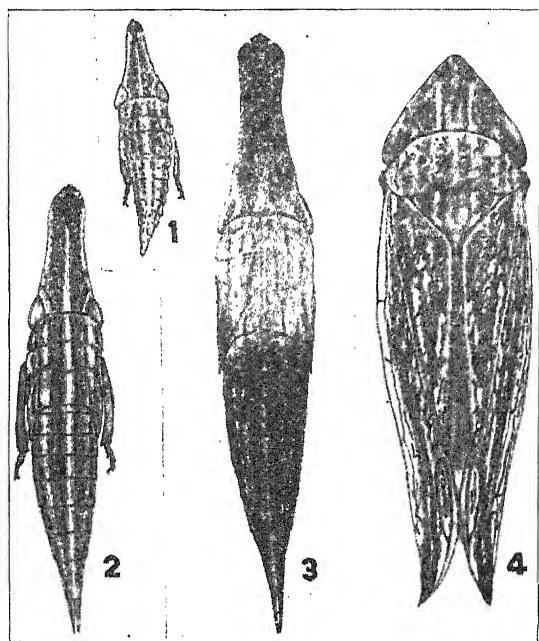
Similar to preceding with abdomen much longer proportionately, almost twice as long as vertex. Vertex about one-fourth longer than thorax. Wing pads only slightly visible. The coloration is very similar to the preceding, except that the markings are more pronounced

in this instar. The dark cross on the tip of the vertex is much more conspicuous. Thorax and abdomen with four rather definite brownish longitudinal lines, separating the three pale stripes. Face dark brown to black with similar pale markings, as in preceding instars.

Fifth Instar. (Figure 3).

Length, 9 mm.

In this, the last nymphal instar, the vertex is longer proportionately. It is considerably longer than the thorax and more than one-half as long as the abdomen. The vertex is even more spoon-shaped than in preceding instars and the apical portion is quite concave. The keel on the face is proportionately larger. Coloration darker and more conspicuous than in preceding instars.



Photographs of the various stages of the life cycle.

Fig. 1. Second instar nymph.

Fig. 3. Fifth instar nymph.

Fig. 2. Fourth instar nymph.

Fig. 4. Adult.

Adult. (Figure 4).

Length, 7 mm.

On comparing the adult and last nymphal instar, it will be noticed that the adult is much shorter, which is rather unusual among the *Cicadellidæ*. Furthermore the vertex is greatly shortened and broadened in the adult. It is only slightly longer than the pronotum and is much shorter than the thorax. The conspicuous keel on the face is lost entirely, and one not familiar with the nymphal stages would scarcely place

nymphs and adults of this insect together as the same species. The elytra are well developed and pointed at the apex. The entire insect is marked with brown irrorations or ramose pigment lines.

PHYLOGENETIC RELATIONSHIP.

In regard to relationship, it is our belief that the earlier stages of any animal give more evidence pertaining to its relationship to other species and its ancestry than we are able to judge from the adult condition. The fact that the nymphal forms exhibit a long foliaceous vertex would certainly place this species with the *Dorydiaria*, which is composed of a group of species with this vertex character. Prof. Osborn* placed it in this position without having seen the nymphal stage and the author† after examining the nymph also allied it with the *Dorydiaria*. Van Duzee‡ has placed it intermediate between *Phlepsius* and *Acinopterus*. The resemblance to *Phlepsius* is more or less superficial, but he has evidently placed it here because in coloration it is brownish irrorate and has definite ramose pigment lines especially on the elytra. In this respect it does resemble a species of that genus. It is true, however, that after the vertex is greatly reduced in the adult stage, the head resembles very closely the foliaceous type of *Phlepsius* head. In the nymphal stages of these *Phlepsius* species, however, so far as the author has been able to examine them, there is nothing to compare with the vertex of the *Dorydiella*. It has been placed close to *Acinopterus* no doubt because of the pointed apex of the elytron. The usual condition is a well rounded apex. In the American *Cicadellidæ* this pointed elytron is found in very few genera. In addition to the *Dorydiella* and *Acinopterus* it is also found in *Dorydium*, which is one of the *Dorydiaria*. Furthermore, the nymphs of *Acinopterus* and *Dorydiella* are entirely different, suggesting diverse affinities, and the adults have very little in common except the pointed elytron, so this would seem to indicate parallel development instead of a close relationship and the emphasis should be placed upon the nymphal characters. In view of the fact we have found only one species belonging to this genus we are able to designate relationship only by the characters of the various stages of this species.

* Ohio Journal Sci., Vol. XX, No. 5, p. 160, 1920.

† Bull. 34, St. Geol. & Nat. Hist. Survey, Conn., p. 91, 1923.

‡ Univ. of Calif. Pub., Tech. Bull. Vol. II, 1917, p. 675.

VARIATIONS IN THE ROOT SYSTEM OF THE COMMON EVERLASTING (GNAPHALIUM POLYCEPHALUM).

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It has been observed that the root system of the common everlasting (*Gnaphalium polycephalum*) has a different behavior when it is grown in different habitats. On well-drained, sloping areas the roots show positive geotropism, that is they grow down, while on poorly drained flat areas the roots show plagiotropism or diageotropism, that is they turn at right angles.

The sloping areas from which the roots were collected were well-drained and consequently well aerated; the flats were either clearings or meadows of the uplands and consequently undrained. In these flats the water table was not far from the surface in late fall, winter, and spring (1). The soil was largely Cincinnati silt loam and Clermont silt loam. The Cincinnati silt loam consists of eight to twelve inches of grayish yellow or light yellowish brown silt loam, having a characteristic mealy or velvety feel. This soil plows up readily and is formed by the weathering of loess on rolling uplands along with the aeration of the soil. Clermont silt loam consists of a layer of seven to twelve inches of light gray or nearly white silt loam. When typically developed it is very ashy, and on the flattest, most poorly drained areas iron concretions are frequently scattered over the surface. The subsoil is of an impervious and compact nature. It possesses practically no power of granulation. Clermont silt loam always develops by the weathering of loess on flat uplands, where there is a deficiency of oxygen. The difference between this soil and the Cincinnati silt loam is due entirely to the difference in drainage. Owing to the level character of the surface on which Clermont silt loam is produced and the impervious nature of the subsoil, natural drainage is very deficient. Hence, there is often found water standing on the surface and this prevents aeration. As a result, humic acid is produced and there is the precipitation of lime, iron, and phosphorus of the soil. Since the soil is limestone, this results in acid on limestone soil (4). The flatness together with the fine impervious soil make the flats very wet. Along with

the excess of water in the soil there is a deficiency of oxygen. Therefore, it is probable that the poor drainage together with the deficiency of oxygen caused the everlasting roots growing on flats to turn. It has been reported (5) that roots show aerotropism, that is, when oxygen diffuses against young roots from one side, the root curves toward the source of the gas.

The everlasting is a winter annual. The seeds germinate very soon after ripening in late fall. The rosettes remain through the winter and spring. In the summer the tall stalks and the flowers of the plants develop. The development of the root system precedes this; therefore the tap root must have developed when the water table was near the surface. The high water table at this time probably accounts for the turning of the roots. The factors which determine the turning of the roots may be an excess of water, deficiency of oxygen, or both. A secondary factor resulting from these two may be soil acidity.

SOIL REACTIONS.

Two hundred and twenty-two roots from various areas—steep slopes, gentle slopes, even flats, and irregular flats, or flats made irregular because they had been plowed at some time—were collected in the late fall after growth had been completed. These roots were observed and placed in one of three classes: I, roots showing positive geotropism; II, roots showing diageotropism; III, roots showing less pronounced diageotropism.

In order to determine whether soil reaction is a factor in deciding direction of root growth, at the time the roots were collected, soil samples were taken from above and below the point of turning if the root turned, or at the top and bottom of the root system if the root did not turn. Later the specific acidity or alkalinity of the soils were determined according to the Wherry field method (6). The results of the observations are given below:

I. ROOTS SHOWING POSITIVE GEOTROPISM. (Fig. 1).

Number	Nature of Area	Reaction at Top	Reaction at Bottom
21	gentle slope	neutral	neutral
15	gentle slope	neutral	sp. acid. 30+
9	gentle slope	sp. alk. 3+	neutral
3	gentle slope	sp. acid. 3+	sp. acid. 3+
16	steep slope	neutral	neutral
16	steep slope	sp. acid. 30+	sp. acid. 30+
1	even flat	sp. acid. 10+	sp. acid. 10+

Of the eighty-one roots showing positive geotropism, eighty of these grew on slopes and one on an even flat. Of these eighty, thirty-two grew on steep slopes (two areas) and forty-eight on more gentle slopes (seven areas). The slopes were well-drained and consequently well aerated.

At the top of the root systems the conditions varied from specific alkalinity 3+ to specific acidity 30+. At the bottom the conditions varied from neutral to specific acidity 30+. From these data it can be seen that there was no relation between the soil reaction and the fact that the roots grew down. Positive geotropism is not due to the specific alkalinity or acidity of the soil.

II. ROOTS SHOWING DIAGEOTROPISM. (Fig. 2).

Number	Nature of Area	Reaction Above Turn	Reaction Below Turn
32	even flat	neutral	neutral
7	even flat	neutral	sp. alk. 10+
7	even flat	sp. alk. 10+	sp. alk. 10+
4	even flat	sp. acid. 10+	sp. acid. 10+
12	even flat	sp. acid. 30+	sp. acid. 30+
6	even flat	sp. acid. 100+	sp. acid. 100+
7	irregular flat	neutral	sp. acid. 30+
6	slope	neutral	sp. acid. 3+

Of the eighty-one roots that showed diageotropism, seventy-five grew on poorly drained flats and six on a slope. Of these seventy-five, sixty-eight grew on even flats (nine areas) and seven on an irregular flat. The slope on which the six roots grew was the extreme base of a steeper slope, and hence almost a flat. Therefore, the water table was not far from the surface.

III. ROOTS SHOWING LESS PRONOUNCED DIAGEOTROPISM. (Fig. 3).

Number	Nature of Area	Reaction Above Turn	Reaction Below Turn
10	even flat	neutral	neutral
1	even flat	neutral	sp. alk. 3+
4	even flat	sp. alk. 10+	sp. alk. 10+
5	even flat	sp. acid. 10+	sp. acid. 10+
5	even flat	sp. acid. 30+	sp. acid. 30+
6	even flat	sp. acid. 100+	sp. acid. 100+
3	irregular flat	neutral	sp. acid. 30+
6	gentle slope	neutral	neutral
7	gentle slope	neutral	sp. acid. 3+
9	gentle slope	neutral	sp. acid. 30+
4	steep slope	neutral	neutral

Above the turn of the roots, the conditions varied from specific alkalinity 10+ to specific acidity 100+. Below the turn, the conditions varied from specific alkalinity 10+ to specific acidity 100+. As there is such wide variation in soil reactions, it seems evident that diotropism is not due to the specific alkalinity or acidity of the soil.

Of the sixty roots that showed less pronounced diageotropism, thirty-four grew on flats and twenty-six on slopes. Of these thirty-four on flats, thirty-one were found on even flats (nine areas) and three on an irregular flat. Of the twenty-six on slopes, twenty-two grew on very gentle slopes (five areas) and four on a steep slope. The slopes were gentle, with the exception of one, so that in them the water tables were not far from the surface, though lower than on the flats.

Above the turn of the roots, the conditions varied from specific alkalinity 10+ to specific acidity 100+. Below the turn, the conditions varied from specific alkalinity 3+ to specific acidity 100+. Hence, as before, there is no relation between soil reaction and diageotropism.

EXPERIMENTAL GROWING OF SEEDLINGS.

From field observations on the root systems of the common everlasting, it was not possible to determine whether diageotropism of roots in poorly drained areas was due to an excess of water in the soil, to a deficiency of oxygen, or to both. The growing of seedlings under controlled conditions in the laboratory was undertaken in order to separate these two factors.

It proved to be unsatisfactory to grow seedlings of the everlasting because of the extremely small size of the young plants, and also because the short period of viability made it impossible to make consecutive plantings. For this reason, a number of other plants were substituted. These were sunflower, *Helianthus annuus*, chosen because of its rapid growth and therefore short observation period; three varieties of tomato, Globe Tomato, Chalk's Early Jewel Tomato, and Trucker's Favorite Tomato, chosen because the tomato is one of the important truck crops of the undrained upland flats; and *Bidens aristosa*, a plant abundant in some of the upland flats (2).

Seedlings of these plants were grown under three conditions: I, in well-drained soil; II, in soil with excess of water; III, in soil with excess of water, into which air was introduced. In all cases the soil used showed a specific alkalinity of 10+.

I. Plants grown in well drained soil.

(Figs. 4-5.)

Seeds were planted about one inch deep in ordinary flower pots and germinating boxes which were supplied with good bottom drainage and kept only moist enough to insure germination and prevent wilting. The results were as follows:

TABLE SHOWING CHARACTER OF ROOT GROWTH IN WELL-DRAINED SOIL.

Name of plant	No. days to appear above ground	Days in soil after above ground	No. of plants examined	Character of root-growth
Pot 1 Sunflower	4	8	6	Down, few short laterals
Pot 2 Sunflower	4	10	3	Down, almost no laterals. (Fig. 4)
Pot 3 Sunflower	4	10	5	Down, three plants: numerous long laterals; two plants: short roots and few short laterals
Pot 4 Sunflower	6	8	5	Down, numerous long laterals
Pot 5 Sunflower	6	8	4	Down, numerous long laterals
Pot 6 Sunflower	7	19	6	Down, numerous long laterals (Fig. 5)
Pot 7 Globe Tomato	13	8	6	Down; single tap; no laterals
Pot 8 Trucker's Favorite Tomato	15	34	15	Down, single tap root
Pot 9 Bidens aristosa	15	36	6	Down, fine roots
Pot 10 Chalk's Early Jewel Tomato	15	41	18	Down; long tap root, few laterals

Seventy-four plants were removed from the pots and examined. The roots of all of them showed positive geotropism, (Figs. 4-5). Of these seventy-four roots, twenty-nine were sunflowers, thirty-nine were tomatoes (6 Globe, 15 Trucker's, 18 Chalk's Early Jewel Tomatoes), and six were *Bidens aristosa*. Of the twenty-nine sunflowers, eleven had few or no laterals, (Fig. 4), while eighteen had numerous long laterals, (Fig. 5). Of the thirty-nine tomatoes, the six Globe and the fifteen Trucker's Tomatoes had single tap roots, and the eighteen Chalk's Early Jewel Tomatoes had long tap roots and few laterals; the six *Bidens aristosa* had few laterals. There was no change in soil reaction during the growth of the plants. From these results, the conclusion is drawn that plants grown in well-drained soil develop positively geotropic single tap roots with comparatively few or no laterals.

II. Plants grown in soil with excess of water.

(Fig. 6.)

Seeds of the same kinds as were planted in well-drained pots in Group I were planted in pots which were placed in a large pan filled with water having a constant level. Thus a high water table one and one-half inches below the soil surface was produced. Water was constantly flowing out through an overflow. The results are shown in table on following page.

Thirty-two plants were removed from the pots and examined. All the roots showed diageotropism, turning at the water level, (Fig. 6). Of these thirty-two roots, seventeen were sunflowers, twelve were tomatoes (eight Globe, two Trucker's, two Chalk's Early Jewel Tomatoes) and three were *Bidens aristosa*. The seventeen sunflowers (Fig. 6) had numerous, long laterals, while the three kinds of tomatoes and *Bidens aristosa* developed tap roots with no laterals. There was no change in soil reaction during the growth of the plants. It has been found by other workers (3) that *Helianthus* plants undergo a retardation in growth in length of their main roots when cultivated in water. In the case of the plants grown under poor drainage conditions, there are two factors involved that might have caused the roots to turn: First, excess of water, and second, lack of oxygen.

TABLE SHOWING CHARACTER OF ROOT GROWTH IN SOIL WITH EXCESS OF WATER.

Name of plant	No of days to appear above ground	Days in soil after above ground	No. of plants examined	Character of root-growth
Pot 1 Sunflower	7	5	2	Tap root turns at right angles; numerous long laterals(Fig.6)
Pot 2 Sunflower	7	7	3	Turn,numerous long laterals
Pot 3 Sunflower	4	10	3	Turn,numerous long laterals
Pot 4 Sunflower	6	8	2	Turn,numerous long laterals
Pot 5 Sunflower	6	8	2	Turn, long laterals
Pot 6 Sunflower	7	19	5	Turn,numerous laterals
Pot 7 Globe Tomato	13	8	8	Turn
Pot 8 Truckers Favorite Tomato	15	34	2	Turn, single tap root; no laterals
Pot 9 Bidens aristosa	20	31	3	Turn
Pot 10 Chalk's Early Jewel Tomato	15	41	2	Turn, poorly developed

III. Plants grown in soil with excess of water, into which air is introduced.

(Fig. 7.)

In order to separate the two factors which may have been responsible for the turning of the roots under poor drainage conditions, seeds were planted under high water table conditions, but air was introduced into the pots. From the air pump there was a hose leading through a paraffined cork into an air-tight bottle. From this vessel, air was conducted to

the bottom of each of two pots, by means of rubber tubing connecting with L-shaped tubes, which opened at the bottom of the pot. The open ends of the glass tubes were protected with cheese cloth. Air thus passed upwards through the soil. The two pots and the air container were placed in water and thus a high water table one and one-half inches below the soil surface was produced. The seeds were planted one and one-half inches below the top of the pot and one inch below them was the water table. Thus, the seeds were grown under poor drainage conditions, but did not lack air. The results were as follows:

TABLE SHOWING CHARACTER OF ROOT GROWTH IN SOIL WITH EXCESS WATER INTO WHICH AIR IS INTRODUCED.

Name of plant	No. of days to appear above ground	Days in soil after above ground	No. of plants examined	Character of root-growth
Pot 11 Sunflower	6	8	6	Down, long tap, numerous long laterals (Fig. 7)
Pot 12 Sunflower	6	8	5	Down, numerous long laterals
Pot 13 Sunflower	6	8	6	Down, long tap, long laterals
Pot 14 Sunflower	6	8	6	Down, three plants; long laterals; three plants; short laterals
Pot 15 Chalk's Early Jewel Tomato	18	22	6	Down, single tap, no laterals

Twenty-nine plants were removed, twenty-three of which were sunflowers, and six were Early Jewel Tomatoes. All the roots showed positive geotropism, penetrating the soil below the water level, (Fig. 7). Of the twenty-three sunflowers, twenty had long tap roots and numerous, long laterals, and three had short or no laterals. The Chalk's Early Jewel Tomatoes had single tap roots and no laterals. It has been found by other workers (3) that the rate of growth in roots of *Helianthus* was faster when atmospheric air was bubbled through a solution.

There was no change in soil reaction during the growth of the plants.

All the roots grown with excess of water and lack of air showed diageotropism; while all the roots grown with excess of water through which air was continuously bubbling showed positive geotropism. Therefore, it was the lack of air in the soil that caused the roots to turn.

The controlled conditions produced in the laboratory were similar to those in the field. The roots of the everlasting growing on well-drained, sloping areas showed positive geotropism. The roots grown under good drainage conditions in the laboratory also showed positive geotropism. The roots of the everlasting growing on poorly drained flats with excess of water in the laboratory also showed diageotropism. In the case of the roots that turned, both in the field and in the laboratory, the conditions of growth were similar. In the field the roots were found on undrained flats. The flatness, together with the fine, impervious clay soil made the flats very wet. Along with the excess of water in the soil there was a deficiency of oxygen. But it has been shown in the laboratory that when air was supplied to soil with an excess of water, the roots did not show diageotropism, but instead showed positive geotropism. Hence we conclude that it was the lack of oxygen in the soil that caused the roots of the common everlasting growing on poorly drained flats to show diageotropism.

In conclusion, I wish to extend my appreciation for the suggestions and help given by Dr. E. Lucy Braun, of the Department of Botany, University of Cincinnati.

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- Figure 1. Roots of everlasting showing positive geotropism.
 Figure 2. Roots of everlasting showing diageotropism.
 Figure 3. Roots of everlasting showing less pronounced diageotropism.
 Figures 4-5. Roots of sunflowers grown in well-drained soil show positive geotropism. Fig. 4, Sunflower showing positive geotropism and with few laterals; Fig. 5, Sunflower showing positive geotropism and with long, numerous laterals.
 Figure 6. Roots of sunflower grown in soil with excess of water show diageotropism and numerous long laterals.
 Figure 7. Roots of sunflowers grown in soil with excess of water into which air is introduced show positive geotropism.

THE OHIO JOURNAL OF SCIENCE

VOL. XXIV

SEPTEMBER, 1924

No. 5

REPORT OF THE THIRTY-FOURTH ANNUAL MEETING OF THE OHIO ACADEMY OF SCIENCE

The Thirty-fourth Annual Meeting of The Ohio Academy of Science was held at the Ohio State University, Columbus, April 18 and 19, 1924, under the Presidency of Prof. Kirtley F. Mather. One hundred and fourteen members were registered as in attendance; fifty-nine new members were elected.

GENERAL PROGRAM.

FRIDAY, APRIL 18.

- 9:30 A. M.—Business Meeting.
- 10:30 A. M.—Reading of Papers in General Session.
- 2:00 P. M.—The Invitation Address by Dr. Albert P. Mathews, of the University of Cincinnati, on "How Shall We Measure the Quantity of Life?"
- 3:00 P. M.—Reading of Papers in Sectional Meetings.
- 6:30 P. M.—Annual Banquet, Ohio Union, followed by an address of welcome by Dean William McPherson, Ohio State University, with response by Dr. Edward L. Rice, Ohio Wesleyan University.
- 8:00 P. M.—Address by the President of the Academy, Prof. Kirtley F. Mather, Denison University, on "Geologic Factors in Organic Evolution," Campbell Hall Auditorium.

SATURDAY, APRIL 19.

- 9:00 A. M.—Adjourned Business Meeting.
- 10:30 A. M.—Reading of Papers in General Session and in Botany Section.
- 2:00 P. M.—Reading of Papers in Sectional Meetings and Demonstrations.

MINUTES OF BUSINESS MEETINGS.

The first business session was called to order by President Mather at 9:45 A. M. on Friday, April 18, 1924, and an adjourned session was held at 9:00 A. M. on the following day.

The President announced the appointment of the following committees for the meeting:

Committee on Membership—Dwight M. DeLong, Lewis H. Tiffany, Raymond J. Seymour, Harold E. Burt, Frederick C. Blake.

Committee on Resolution—Albert P. Weiss, E. L. Moseley, Edgar N. Transeau.

Committee on Necrology.—Herbert Osborn,

The following *Auditing Committee* was elected by the Academy: Geo. D. Hubbard and H. C. Beardslee.

The following *Nominating Committee* was elected by the ballot of the Academy: Raymond C. Osburn, Lewis H. Tiffany, Geo. D. Hubbard, Raymond J. Seymour, Harold E. Burt, Frederick C. Blake.

Report of the Secretary.

The following report by the Secretary was received and ordered filed.

COLUMBUS, O., April 18, 1924.

To the Ohio Academy of Science:

The year now closing marks a change, as you know, in the Secretariate of the Academy and your Secretary has the distinct conviction that he would be untrue to the real feelings of the members of the Academy, certainly to his own, if he were to allow this fact to pass unnoticed, even if such a thing were possible. Of course all present miss from its accustomed place the genial face of the former Secretary, Dr. Edward L. Rice. During the eleven years of faithful service Dr. Rice not only made a real contribution to the Academy but made himself so useful, so helpful, not to say indispensable, that in the minds of many of us the names "Ohio Academy of Science" and "Edward L. Rice, Secretary" are almost synonymous. But words are unnecessary: "His works do praise him."

It is only fair to say, also, that the work of the former Secretary did not end with the election of his successor, since upon him fell the duty, for example, of clearing up the odds and ends after the Annual Meeting at Oberlin in March, of preparing the Annual Report for the printer, of notifying newly-elected officers, members and fellows, of sending out copies of resolutions passed at the last Annual Meeting, and of preparing a report of the meeting for *Science*, etc. It was therefore early in July before the complete and formal transfer of the archives was made

and even then the former Secretary was not entirely released, as we have freely availed ourselves of his generous offer to lend assistance at any time and in any way possible.

Furthermore it should be stated that *the Secretariate was turned over in an excellent, up-to-date condition.*

The first item of more than routine importance to claim the attention of the new Secretary was the publication in pamphlet form of a memoir of the late Emerson McMillin, referred to on page 281 of the Proceedings of the Thirty-third Annual Meeting. Some 50 copies of this memoir were published by the Academy and distributed to the family and selected friends of Mr. McMillin.

The next item of general interest to the Academy was an invitation from the Ohio Forestry Association, through its Secretary, Prof. Edmund Secrest, inviting the members of the Academy to participate, as guests of the Association, in a field meeting at the John Bryan Park on September 21 and 22, 1923. This invitation was passed on to the members of the Academy in a letter dated September 8, 1923. Several members of the Academy availed themselves of this very courteous invitation, much to their pleasure and delight, and one or two of our members appeared on the program put on by the Association.

Owing to the sudden and unexpected passing away of our most distinguished member, the late Dr. T. C. Mendenhall, on March 22, 1924, the Secretary assumed the authority to call Dr. E. L. Rice over the long distance telephone and request him to represent the Academy at the funeral services held at Ravenna. This he consented to do and did. This action has since been approved by the Executive Committee.

The routine work of the office has been about as usual and very considerable; details have been taken care of as promptly and as efficiently as possible under the circumstances.

The generous, helpful cooperation of all the officers of the Academy has been a source of real inspiration throughout the year, for which hearty thanks are due and hereby recorded.

WILLIAM H. ALEXANDER, *Secretary.*

Report of the Treasurer for the Year 1923-1924.

The following report by the Treasurer was received and referred to the Auditing Committee whose report is appended.

To the Ohio Academy of Science:

The Treasurer submits the following report for the period from March 26, 1923, to April 2, 1924:

RECEIPTS.

Cash balance on hand March 26, 1923.....	\$766.05
Librarian's sales of publications.....	37.97
Interest on certificate of deposit.....	19.50
Members dues, paid through the A. A. A. S. and directly to the Treasurer.....	709.14

Total receipts.....\$1,532.66

DISBURSEMENTS.

American Association for the Advancement of Science.....	\$ 76.00
Columbian Building and Loan Association, for deposit.....	750.00
H. C. Cowles, traveling expenses.....	30.00
E. L. Rice, secretarial and traveling expenses.....	10.78
Earl Sheffel, refund.....	2.00
Independent Print Shop.....	29.00
Spahr & Glenn, Printers.....	3.25
A. E. Kraus, Print Shop.....	32.00
Herbert Osborn, traveling expenses.....	13.50
Wm. Alexander, secretarial expenses.....	18.15
Eunice McCray, stenographic service.....	10.00
Helen M. Coleman, stenographic service.....	3.25
Total Disbursements.....	\$ 977.93
Cash balance on hand April 2nd, 1924.....	554.73
Assets—Certificate of deposit for.....	650.00
Total Assets.....	\$1,204.73

The original purchase of a certificate of deposit for \$750.00 was later reduced \$100.00 to pay the honorarium to the Academy Secretary. It will be noted that this item does not appear above. Cancelled checks and vouchers are herewith submitted with the books.

Dr. Burton E. Livingston, Permanent Secretary of the A. A. A. S., reported that the plan of having joint dues in the Academy and the A. A. A. S. payable through his office was working satisfactorily.

Respectfully submitted,

A. E. WALLER, *Treasurer.*

Books, checks and vouchers submitted and found to be correct.

GEO. D. HUBBARD,
H. C. BEARDSLEE,
Auditing Committee.

Report of the Executive Committee.

The following report of the Executive Committee was received and ordered filed.

COLUMBUS, O., April 18, 1924.

To the Ohio Academy of Science:

A meeting of the Executive Committee was held in Columbus on November 9, 1923, with all members present except the President, who because of absence from the State could not attend the meeting. By invitation Vice-President Barrows and Prof. Raymond C. Osburn were present, the former presiding over the meeting.

A letter was read from President Mather, extending greetings and good wishes and suggesting among other things that some action should be taken regarding the expenses of Prof. Herbert Osborn as the duly accredited representative of the Academy to the Leidy Commemorative Meeting to be held in Philadelphia on December 6, 1923. Thereupon the committee instructed the Treasurer to reimburse Professor Osborn for all necessary expenses incurred in this connection.

The Secretary was requested and authorized to make such arrangements as might seem wise in the establishing of temporary headquarters for the visiting members of the Ohio Academy at the annual meeting of of the American Association for the Advancement of Science to be held in Cincinnati the latter part of December, 1923. This action was very satisfactorily carried out through the generous cooperation of members of the Academy living in Cincinnati.

At this meeting of the committee it was decided to accept the invitation of the Ohio State University to hold the Thirty-fourth Annual Meeting of the Academy at that institution. It was also agreed that the time should be "very near Easter" but the exact date was left for the Secretary to determine after some further investigations.

A second meeting of the Executive Committee was held in Columbus at the office of the Secretary last evening with all members present.

At this meeting forty applications for membership in the Academy were approved subject to final ratification by the Academy.

The Secretary placed before the committee a cordial invitation from the Faculty of the College of Wooster, heartily seconded by the staff of the Ohio Agricultural Experiment Station, to hold the next Annual Meeting of the Academy at Wooster. The committee decided to refer the invitation to the Academy for such action as it may see fit to take.

The following letter from Dr. Burton E. Livingston, Permanent Secretary, American Association for the Advancement of Science, written in reply to a letter inviting Dr. Livingston or some other officer of the A. A. A. S. to be present at the Annual Meeting of this Academy, was laid before the committee, viz.:

WASHINGTON, D. C., March 18, 1924.

DEAR MR. ALEXANDER:—I have your letter of March 10 and have read it with much interest. It is the plan of the American Association to have, whenever possible, a representative of the Association in attendance at each annual meeting of the affiliated academies. This was decided at the Cincinnati meeting. But the whole question of the arrangements with affiliated academies has recently come up again for discussion and we think it will be best not to begin naming official representatives for academy meetings till the Executive Committee has had opportunity to define the attitude of the Association in regard to affiliated academies in a manner clearer than has thus far been done. We are making a serious study of the whole problem of academy affiliation and it may be possible that some improvements can be introduced. When we do begin to send representatives to the academy meetings, those representatives should naturally have the whole matter clearly in mind, and that could not be the case at present. There will doubtless be important matters to be discussed with the several academies.

I hope you will understand from this why I feel that we should postpone till a later time our beginning to name official representatives for the academy meetings.

I should like nothing better than to come to your meeting myself and I hope to be able to do so next year, perhaps.

Thanking you, and with all good wishes for the great success of your meeting,

Yours very sincerely,

BURTON E. LIVINGSTON,
Permanent Secretary.

The following communication was received from Charles E. Deam, President of the Indiana Academy of Science, and referred to the Academy for action, viz.:

BLUFFTON, IND., April 9, 1924.

DEAR MR. ALEXANDER:—I am sorry I shall not be able to attend the meeting of the Ohio Academy of Science April 18 and 19.

I wish if you do so, you would extend a most cordial invitation to all members of the Ohio Academy of Science to meet with the Indiana Academy of Science at their spring meeting to be held at Marengo, Ind., May 15–17.

At this meeting those who wish may go through the Marengo Cave at Marengo, and on the second day may go through Wyandotte Cave, about 13 miles distant. The field trips will be very interesting to the botanist and the geologist. The leader of the botanical section is well acquainted with the area and will show such rare plants as *Isoetes Engelmannii*, *Smilax Bona-nox*, and many others that are extremely local. The geologists will be led by one who has walked the entire region and is well acquainted with it. Come in hiking clothes.

Yours most cordially,

CHAS. C. DEAM.

An invitation was read from the President and Secretary of The Franklin Institute, Philadelphia, Pa., to participate in the celebration on September 17, 1924, of the *Centenary* of the signing of the Act of Incorporation of the Institute, by the appointment of a representative; this invitation is also referred to the Academy for action.

An invitation was also read from the British Association for the Advancement of Science, inviting members of this Academy to attend its Annual Meeting to be held in Toronto from August 6 to 13, 1924. Your Executive Committee suggests the names of Dr. A. E. Waller and Dr. Edward L. Rice as delegates to this meeting.

Respectfully submitted,

WILLIAM H. ALEXANDER,

For the Committee.

Report of the Publication Committee.

The following report of the Publication Committee was received and ordered filed:

The Annual Report of the Thirty-third Meeting, Proceedings, Vol. VII, Part 8, contained 29 pages and was published November 26, 1923. The report minus the membership list was also published in the *Ohio Journal of Science*: 23: 209-234, 1923.

Respectfully submitted,

H. C. SAMPSON, *Chairman.*

Report of the Library Committee.

The following report of the Library Committee was received and ordered filed:

COLUMBUS, O., April 18, 1924.

To the Ohio Academy of Science:

The Library Committee begs to report that all duties devolving upon it have been discharged as promptly as possible.

The sale of publications during the year amounted to \$37.97. This amount has been turned over to the Treasurer of the Academy.

The Proceedings of the Thirty-third Annual Meeting, 1923, were received from the printer in December and copies were mailed to all members of the Academy and to the exchanges early in the year 1924.

The publications received by the Academy on exchange have been added to the sets filed in the University Library. The scientific sections of the library have been increased annually by the purchase of many important sets and the hope is expressed that more and more the University Library will serve as the center of scholarly research by members of the Academy.

Respectfully submitted,

C. W. REEDER,

For the Library Committee.

Report of the Trustees of the Research Fund.

The Trustees reported, orally, that owing to the very recent death of their Chairman, Dr. T. C. Mendenhall, who had full charge of the books and records pertaining to the work of the Board of Trustees and usually prepared the report, it had been impossible for the other members to prepare a written report in time for this meeting, or to work out the details of the plan recommended by Dr. Mendenhall and endorsed by the Academy at the last Annual Meeting (see page 282, Proceedings, Thirty-third Annual Meeting) regarding the investment of the Research Fund and the use of the income therefrom. The Board requested another year in which to prepare a report. The request was granted.

A preliminary examination of the bank accounts, made soon after the April, 1924, meeting of the Academy, shows the following: Bills to the amount of \$126.36 were paid subsequent to April 1, 1923, and additions from interest on bonds amounting to \$27.62 have been credited, leaving a cash balance of \$724.82, or a total resource with bonds of \$1,324.82.)

In this connection the Secretary read the following letter written by Dr. Mendenhall only three days before his death:

RAVENNA, O., March 19, 1924.

MY DEAR MR. ALEXANDER:

Yours of the 17th has reached me together with another communication from you of an earlier date, which I found awaiting me on my arrival from Columbus on last Saturday night. You are perhaps by this time aware that I have been in the City of Columbus for the last two weeks, the victim of the ingenuity and indefatigable zeal of the doctors,

who have been doing everything that they can for me, or rather, I should say to me and eventually for me.

However, the investigation with all that has gone along with it has fatigued me very much and I was glad to reach home Saturday night. Now this has been a painful and possibly serious affair with me, and therefore, you will see that I must at once abandon all attempts to do anything for the Academy of Science for some time to come.

I regret this very much as there are several things which should be looked after in regard to the Emerson McMillin Fund. Not one single transaction has taken place so the financial situation is precisely as I have reported plus, of course, the income from our invested funds, so it will be very easy to determine approximately what amount will be available on the 19th of April. I hope to be able to prepare something in the form of a report by that time.

Yours faithfully,

T. C. MENDENHALL.

Upon motion duly made and carried, the Trustees were instructed to conserve the income from the McMillin Fund during the ensuing year.

Report of the Committee on State Parks and Conservation.

The Chairman of the Committee, Prof. Herbert Osborn, stated that the committee had not succeeded in having any formal meetings as it is made up, very properly, of members scattered through the State and there had been no convenient occasion on which to get the members together. It is of interest to report, however, that there has been distinct progress in the matter of reservations for park, game refuge and forestry purposes which have materially extended the areas devoted to these purposes and which we may count as distinct advances. The Bryan State Park which includes part of the Clifton Gorge and which was mentioned in our last report as likely to be finally accepted by the State has now definitely become State property and is administered by the State Experiment Station, so that it may be counted as permanently devoted to park and reservation purposes and its scenic, biologic and geologic features preserved for future students.

At a meeting of the State Forestry Society last September, to which our members were invited, as pointed out in the Secretary's Report, we had an opportunity to observe the conditions and possibilities there under very favorable circumstances.

The Roosevelt Game Refuge, now embracing some 15,000 acres, was dedicated last fall and is already proving its value in stimulating interest and activity in the preservation of the native plants and animals of the region. Additional tracts have been secured for the state forests and these have distinct value as areas in which conditions will serve to perpetuate our native fauna and flora. The park system of Cleveland, which was visited with the kind guidance of Professor Fullmer, gives very encouraging evidence of a broad plan for the development of adequate park areas including some remarkably fine natural scenery and the preservation of natural conditions for plant and animal life.

The publication of the Naturalists Guide by the Ecological Society of America and for which the Ohio areas have been very carefully listed by Dr. E. Lucy Braun, is expected in the near future and will make available to our members a detailed list of tracts now reserved or which should be made into reservations when possible. There is a manifest interest in this subject in many of the states and great progress has been made in some of our sister states, notably New York and Iowa, and we may expect a growing appreciation of its importance and efforts of the Academy should be continued in order that the scientific aspects may receive proper attention.

This statement by the chairman of the committee was received as a report of progress and the committee continued.

Report of the Committee on Legislation.

The chairman of the Committee made an oral statement to the effect that in as much as the General Assembly failed to pass the bill (H. B. No. 400) that was before it at the time of our last meeting and as there has been no session of the Assembly since that time, the committee has not been able to do anything more than "watchful waiting." This statement was received as a report of progress and the committee continued.

Election of Officers.

The following officers and committee members for 1924-25 were elected by the ballot of the Academy.

President—Prof. Edgar N. Transeau, Ohio State University, Columbus.

*Vice-Presidents:**Zoology*—Ralph V. Bangham, Wooster College, Wooster.*Botany*—Prof. Edmund Secrest, Ohio Agricultural Experiment Station, Wooster.*Geology*—Prof. G. W. Conrey, Ohio State University, Columbus.*Medical Sciences*—Prof. R. G. Hoskins, Ohio State University, Columbus.*Psychology*—Prof. F. C. Dockeray, Ohio Wesleyan University, Delaware.*Physical Sciences*—Prof. C. D. Coons, Denison University, Granville.*Secretary*—William H. Alexander, U. S. Weather Bureau, Columbus.*Treasurer*—Dr. A. E. Waller, Ohio State University, Columbus.*Elective Members of the Executive Committee*—Prof. C. G. Shatzer, Springfield; Prof. Bradley M. Patten, Cleveland.*Member Publication Committee*—Prof. Lewis G. Westgate, Delaware.*Trustee Research Fund*—Dr. Edward L. Rice, Ohio Wesleyan University, Delaware.*Member of Library Committee*—Prof. Frederick C. Blake, Ohio State University, Columbus.*Legislative Committee*—Wm. H. Alexander, Columbus; M. M. Metcalf, Oberlin; Paul M. Rea, Cleveland; Edward L. Rice, Delaware; L. B. Walton, Gambier.*Representatives on Editorial Board of Ohio Journal of Science:**Zoology*—Prof. R. A. Budington, Oberlin College, Oberlin.*Botany*—Prof. Bruce Fink, Miami University, Oxford.*Geology*—Prof. G. D. Hubbard, Oberlin College, Oberlin.*Medical Sciences*—Prof. F. C. Waite, Western Reserve University, Cleveland.*Psychology*—Prof. H. A. Aikins, Western Reserve University, Cleveland.*Physical Sciences*—Prof. S. J. M. Allen, University of Cincinnati, Cincinnati.*Election of Members.*

The following persons were regularly nominated and elected to membership in the Academy:

ALDERMAN, OVID A.; Botany, Zoology; 308 Bowman St., Wooster.

BARTHOLOMEW, PAUL S.; Botany, Entomology, Ornithology; R. F. D. No. 3, Sycamore.

BEARSS, ESTHER; Biology; Cochran Hall, Westerville.

BEAVER, WILLIAM C.; Zoology, Medical Sciences, Botany; Head of Department of Biology, Wittenberg College, Springfield.

BILSING, S. W.; Entomology, Zoology; College Station, Texas.

BUSCH, K. G. A.; Chemistry, Botany; Capital University, Columbus.

CAMP, WENDELL H.; Geology, Zoology; Otterbein College, Box 101, Westerville.

- CASKEY, MARION W.; Zoology; Ohio State University, Columbus.
CONGER, ALLEN C.; Zoology; Darlington Road, Delaware.
DEHUS, DELORES; Biology; 714 S. Main St., Ada.
DICKERSON, BESSIE; Zoology, Medical Sciences; New Concord.
DIETZ, DAVID; Astronomy, Physics; The Cleveland Press, Cleveland.
EDWARDS, LINDEN FOREST; Zoology; Reynoldsburg.
GAMBRELL, FOSTER LEE; Entomology, Zoology; Ohio State University, Columbus.
GILLESPIE, J. S.; Geology; 1075 Madison Ave., Columbus.
GOODWIN, HOWARD R.; Archaeology; Ohio State Archaeological and Historical Museum, Columbus.
GOURLEY, J. H.; Horticulture; Wooster.
HALL, SCHULER P.; Physics; Wooster College; Wooster.
HARP, HUGH G.; Astronomy, Meteorology; Wittenberg College; Springfield.
HEATH, A. B.; Physical Geography, Meteorology, Geology; 544 Franklin St., Hamilton.
HEFNER, ROBERT A.; Zoology, Astronomy; 238 W. Tenth Ave., Collmbus.
HENDERSON, A. LEE; Psychology, Medical Sciences; 489 Maynard Ave., Columbus.
HILKER, H. V.; Geology, Archaeology; 325 N. Third St., Hamilton.
JOHNSON, H. M.; Psychology; Ohio State University; Columbus
JONES, MERLIN PERRY; Entomology, Botany; 89 Euclid Ave., Columbus.
KAO, CHUNG KWAI; Botany; 101 W. Eighth Ave., Columbus (Permanent address: Hoking, Yunnan, China).
LAFLEUR, ALBERT; Geography, Geology, Meteorology, History; Box 357, Athens.
LAMBORN, R. E.; Geology; Department of Geology, O. S. U.; Columbus.
LEWIS, GEORGE; Electro and Radio Physics; Crosley Radio Corporation, Cincinnati.
LINDSEY, A. W.; Entomology, Zoology; Denison University, Granville.
LUSK, RALPH G.; Geology; Granville.
MASON, CAPT. PAUL; Archaeology, Meteorology, Public Health; 271 S. Champion Ave., Columbus.
MARTIN, CLARE; Chemistry, Physics; State Normal College, Bowling Green.
MATHEWS, ALBERT P.; Biochemistry, Physiology; University of Cincinnati; 255 Loraine Ave., Cincinnati.
MILLER, DAVID F.; Zoology; 1466½ Pennsylvania Ave., Columbus.
MOON, M'DELLA; Botany, Zoology; 48 Seventeenth Ave., Columbus.
MOSES, C. F.; Geology; Muskingum College; New Concord.
OLSON, HENRY W.; Zoology; 356 Centner Ave., Columbus.
ORR, GROVER L.; Chemistry, Physics; Capital University, 767 College Ave., Columbus.
PALLISTER, JOHN C.; Entomology, Zoology; Cleveland Museum of Natural History, 2717 Euclid Ave., Cleveland.

- PATTERSON, EDNA; Zoology, Entomology, Botany, Astronomy; 130 W. Tenth Ave., Columbus.
- PETERSON, CHARLES J.; Botany, Horticulture; Peterson Nurseries Co., Wilmington.
- POLLITZ, LOUISE C.; Geology, Geography, Ecology; Cleveland Museum of Natural History, Cleveland.
- REEVES, PRENTICE; Psychology, Medical Sciences; 208 N. Sandusky St., Delaware.
- RICKEY, EDNA; Psychology, Medical Sciences; 53 Smith Place, Columbus.
- ROFKAR, WILLIAM F.; Zoology, Botany, Geology; 504 Beall Ave., Wooster.
- SCHRADIECK, HENRY E.; Ichthyology, Fish Culture; Urbana University, Urbana.
- TILFORD, PAUL E.; Botany, Chemistry; Ohio Agricultural Experiment Station, Wooster.
- TUTTLE, W. W.; Physiology, Psychology; Bremen.
- VER STEEG, CARL; Geology, Geography; 324 Nold Ave., Wooster.
- WARTERS, MARY; Zoology, Entomology, Botany, Chemistry, Anatomy; 130 W. Ninth Ave., Columbus.
- WEATHERBY, BENJAMIN B.; Physics; Toledo University, Toledo.
- WELTON, F. A.; Agronomy; Ohio Agricultural Experiment Station, Wooster.
- WHITE, GEO. W.; Geology; 86 E. Lincoln St., Westerville.
- WILSON, IRA T.; Zoology; Heidelberg University, Tiffin.
- YEE, MARTIN A.; Medical Sciences, Biology; University of the City of Toledo, Toledo.
- YOUNG, H. C.; Botany; Ohio Agricultural Experiment Station; Wooster.
- ZINKE, STANLEY G.; Meteorology, Ecology, Medical Sciences; 1814 Vine St., Cincinnati.
- ZINZON, W. A.; Physics; New Concord.

Report of the Committee on Election of Fellows:

The following report of the Committee on Election of Fellows was accepted and ordered filed:

COLUMBUS, O., April 18, 1924.

To the Ohio Academy of Science:

A meeting of the Committee on the Election of Fellows was held last evening in Columbus at the office of the Secretary. Eight members of the committee were present, one was represented by proxy, and two were absent without representation.

Of the candidates considered, fourteen received the necessary nine favorable votes and were declared elected. The fellows elected will be personally notified, and the list will be published in the Proceedings.

Respectfully submitted,

WILLIAM H. ALEXANDER, *Secretary.*
For the Committee.

The following is a list of those elected to fellowship:

RALPH V. BANGHAM	LAWRENCE L. HUBER
JOHN W. BARINGER	THOMAS G. PHILLIPS
SAMUEL WOOD CHASE	EDMUND SECREST
GUY W. CONREY	ERNEST RICE SMITH
FLOYD CARLTON DOCKERAY	PARIS B. STOCKDALE
H. A. GOSSARD	HERBERT ANDERSON TOOPS
ROY GRAHAM HOSKINS	CHARLES J. WILLARD

Resolutions.

The following resolutions were unanimously adopted by the Academy:

1. The Academy wishes to thank the members of the Local Committee and the officers of the Ohio State University for the efforts they have made and the courtesies they have extended toward making the Thirty-Fourth Annual Meeting of the Ohio Academy of Science a success.

2. The Academy wishes to express to Dr. Albert P. Mathews, Professor of Biochemistry at the University of Cincinnati, its appreciation of the special lecture on "How Shall We Measure the Quantity of Life?"

3. The Academy wishes to express its endorsement of the resolutions submitted to the United States Congress by the American Ecological Society, to set aside the Glacier Bay region as a National Monument.

Report of the Committee on Necrology.

The following report of the Committee on Necrology was adopted by the Academy and ordered filed:

MEMORIAL TO DR. THOMAS CORWIN MENDENHALL.

The Ohio Academy of Science mourns today a trusted leader and former president, Thomas Corwin Mendenhall. He was eminent in Physical Science as an investigator, a teacher, an expositor and an organizer. The Franklin Institute of Philadelphia in granting to him in 1918 the Franklin medal, "founded for the recognition of those workers in physical science, * * * * * whose efforts have done most to advance a knowledge of physical science" made their award "in recognition of his fruitful and indefatigable labors in physical research, particularly his contribution to our knowledge of physical constants and electrical standards." This was one of a long series of similar awards, crowning his fifty years of leadership in Science.

Born at Hanoverton, Ohio, October 4, 1841, and living till March 22, 1924, his life covered one of the most eventful periods of human history and his scientific career was coincident with many of the most striking developments of modern science.

His earliest scientific paper was published in 1870. For the succeeding thirty years his contributions to the leading scientific periodicals were frequent and important. The Proceedings of the A. A. A. S., the American Journal of Science, Popular Science Monthly, Science, and the U. S. Coast and Geodetic Survey, were principal avenues of publication.

As the first professor of physics of the Ohio State University, the pioneer work of equipping and putting into service a laboratory for instruction and research fell to him. He began this work in 1873, the first man elected to the faculty of the newly organized institution.

In 1878 he accepted the task of organizing the Physics department of the Imperial University of Japan at Tokio. He also founded the meteorological observatory there. His research work in Japan included careful measurements of the gravitation constant at Tokio and on the summit of Fujiyama, a determination of the density of the earth and some very accurate work with a Rutherford grating on the lines of the sun's spectrum. The celebrated astronomer, Professor Young of Princeton, pronounced these results as extraordinary. He also helped found the Seismological Society of Japan, which has done more than any other organization to make seismology an exact science.

In 1881 he returned to this country and resumed his work at Ohio State University. In the following year he organized the Ohio State Weather Service. His activity in seismology continued after his return.

In 1884 he became professor in the U. S. Signal Corps at Washington and developed instruments for the study of earthquakes. He also started C. F. Marvin, a former student of his in Ohio and the present distinguished Head of the U. S. Weather Bureau, in this same line of work. Dr. Mendenhall also began at this time an elaborate study of atmospheric electricity.

In 1886 he became president of the Rose Polytechnic Institute. Though a capable administrator he somehow kept up his scientific investigations and published four or five scientific papers during his three years presidency. The National Academy of Sciences also published a large volume on his work during this period in atmospheric electricity.

In 1889 he was made Superintendent of the U. S. Geodetic Survey. He here developed the famous "Mendenhall half-second pendulum," which for more than 25 years continued to do extraordinarily accurate work in fifteen Survey stations, and is still relied upon for the most exact results. One of these instruments was carried to Alaska; repeatedly landed in a surf boat for observations and when brought back to Washington gave the same value for "g" that it had given before the journey, to one part in 5,000,000. The reports and bulletins of the Survey contain many of his papers between 1889 and 1894. He was also made Superintendent of Weights and Measures and achieved the important task of putting our national system of weights and measures upon a Metric basis.

In 1893 he was one of five eminent electricians (chosen by mail ballot of 150 leading electrical men) to represent the United States at the International Electrical Congress at Chicago. Differences of opinion

developed there threatened to make agreement upon definitions of the principal electrical units impossible. The Franklin Institute now exhibits a sheet of paper on which Dr. Mendenhall one evening wrote down definitions of the ampere, the volt and the ohm. These he presented next morning to the Chamber of delegates; and the definitions finally adopted are practically identical with his penciled memorandum.

In 1894 he began a seven year service as president of the Worcester Polytechnic Institute.

His work as an investigator and as an organizer of research was indeed notable, but he also had a most unusual gift for making the results of scientific work intelligible and interesting to popular audiences. As a consequence he has been for many years repeatedly called upon for memorial and dedicatory addresses. In 1892 he gave a Convocation Address at Johns Hopkins on "Measurements of Precision, considered in Their Relation to the Condition of Man," and the same year prepared the principal address for the dedication of the new Ryerson Laboratory of the University of Chicago. He gave two series of lectures at the famous Lowell Institute in Boston, one in 1882 and one in 1892. Also lectures at Cooper Union, New York and in Philadelphia, Baltimore and Washington. In 1887 he was made a member of the National Academy of Sciences. In 1888 he was president of the American Association for the Advancement of Science and won golden opinions as presiding officer of the Toronto Meeting. The next year he gave the retiring presidential address at Indianapolis. In 1894 he gave an address as retiring president of the Philosophical Society of Washington. Many of us here remember the delightful address he gave a few years ago as president of our own Ohio Academy of Science and his address on "Some Metrological Memories" before the Franklin Institute in 1918.

His work has been recognized by the award of numerous decorations and medals. From the Paris Exposition in 1900 he received a medal for a monograph entitled "Scientific, Technical and Engineering Education in the United States," from the Imperial Education Society of Japan in 1911 a gold medal. The same year he was decorated with the Order of Sacred Treasures, Japan. The receipt of the gold medal of the Franklin Institute has already been mentioned.

These are but a few of the high points of achievement in a notable career in physical science.

Mention has already been made of his pioneer work in equipping and developing the physical laboratory of the Ohio State University and this is but a small part of his service to that institution. His wise selection of equipment is shown in the fact that many of his early purchases are still giving good service on lecture table and in laboratory. His inspiring leadership of many of the early graduates, such as C. F. Marvin, W. C. Sabine, C. F. Scott, gave them a real start in their notable scientific careers.

Professor Derby, one of his confreres on the faculty in the 80's, has written concerning his important part in determining the educational policy of the institution as follows: "In every faculty certain members are conceded leadership. It soon became plain to me that in questions of

common University concern we usually followed Dr. Mendenhall. In the field of our educational policy he exercised a directive mind. Other professors keen and able in their several subjects, were less attentive to the interests of the institution as a whole, or too individualistic to secure agreement with their suggestions. We were fully awake to the trend of various propositions brought before us and our discussions, though usually courteous, were earnest and now and then sharp in tone. A determination that the work of the institution should be exacting and of high quality was always evident, and any suspected failure to maintain that quality occasioned sharp criticism. In the maintenance of these high standards. Dr. Mendenhall was foremost and his pungent wit seldom missed its mark. When later he withdrew from the University to enter a different scientific field his former colleagues deplored the loss of a beloved comrade, notable scientist and leader in education, but followed his brilliant career with affectionate admiration."

For many years following 1901 a break in health forced him to retire from active scientific and educational work. It was with great satisfaction therefore that some of us heard in June, 1919, that the Governor had appointed him to be a Trustee of the Ohio State University, on the first faculty of which he had served so efficiently many years before. His wise leadership soon caused his election as Chairman of the Board, a position which he greatly honored. His interest in the University never lagged and his faith in its future was evidenced in many ways. One of his last acts was to sign the diplomas for the graduates of the winter quarter of 1924.

In the year 1920, on the occasion of the celebration of the fiftieth anniversary of the founding of the University, Dr. Mendenhall gave to the University a sum of money for the endowment of a gold medal to be known as the Joseph Sullivant Medal. This medal is to be awarded at five year intervals to "that son or daughter of the University who shall have done or have completed, within the five-year period since the last award, a really notable piece of work in either the Liberal, the Fine, or the Mechanic Arts, the pure or applied Sciences, including the various branches of Engineering." The first award was made in 1923 to Mr. Benjamin Garver Lamme, of the Class of 1888.

Dr. Mendenhall's active connection with our Ohio Academy of Sciences began shortly after his return to Ohio in 1912 and he has been a devoted and helpful member interested in promoting its every interest. Almost as soon as he had acquired membership he was elected President, a quite unusual proceeding. This occurred at the Oberlin meeting, 1913, and he served for the year 1914 with such skill and enthusiasm as to give us all renewed courage and confidence in the mission of the Academy.

As Trustee and for a number of years Chairman of the Research Fund of the Academy, serving from 1916 to his death, he was greatly interested in the use of the Academy funds for research and used rare discrimination in the assignment of its limited income to secure the largest benefits in the encouragement of research.

He was particularly interested in the securing of larger support for the Academy and served most faithfully on the legislative committee

which sought state support for Academy activities, especially for publication of the results of scientific studies. He expressed the hope and it was one of his cherished projects that the Academy might sometime be provided with a suitable building for its permanent home and as a center of its activities and that it might serve in some very vital way for the promotion of the scientific functions of the state. His recommendations and suggestions are matters of recent record and may well serve us in our future efforts for the development of scientific activities in the state.

With all these relations the thing that we feel most deeply today is the friendly nature of his work among us. With a most unusual experience in scientific development of more than a half century, a remarkable acquaintance with scientific work and workers he possessed such a broad appreciation of the work and accomplishment of others and such a friendly attitude toward even the most humble worker in the field of science that his presence and interest were a constant source of encouragement. With a multitude of honors and distinctions he was still one of the most democratic and unassuming of men. With a wealth of achievement, seldom equalled, to his credit he was ever modest in reference to the importance of his own contributions to science. He was a man whom we could admire and love, whose friendly greeting will be missed but whose memory will be cherished as representing the finest spirit of scientific devotion, achievement and fellowship. We have recorded our esteem and appreciation of his worth in such honors as it was in our power to give. We have now to place on record, as our lasting recognition of his leadership, this declaration of our high regard for his service, our great indebtedness for his many activities in the Academy and our tribute to his memory as a friend and fellow worker. His fine accomplishments and inspiring personality will long remain with us as a beautiful memory.

HERBERT OSBORN. *Chairman,*
A. D. COLE,
WM. McPHERSON,
Committee on Necrology.

Meeting Place, 1925.

President Mather laid before the Academy the invitation from Wooster College to meet in Wooster next year. Mr. W. C. Devereaux stated that he was fully prepared and authorized to extend an invitation to the Academy to meet in Cincinnati next year but inasmuch as Wooster seemed to have a superior claim in that the Academy had never met in that city, he would withhold his invitation until some future time in favor of Wooster. Whereupon the Academy by vote declared itself in favor of accepting the invitation from Wooster College but left the final decision as to the next meeting place in the hands of the Executive Committee.

Change in Name of Section.

Upon motion of Mr. W. C. Devereaux, seconded by Prof. F. C. Blake, the Academy approved the changing of the name of the section heretofore known as *The Section of Physics* to that of *The Section of Physical Sciences*.

At the suggestion of Dr. E. L. Rice it was unanimously agreed that the passing of this motion would serve also as notice of such changes in the Constitution and By-Laws as might be necessary to conform to said motion.

Delegates to the Toronto Meeting of the B. A. A. S.

By motion duly made and seconded the Academy unanimously approved the recommendation of the Executive Committee that Dr. A. E. Waller and Dr. Edward L. Rice be designated as the duly accredited delegates of this Academy to the Annual Meeting of the British Association for the Advancement of Science to be held in Toronto, August 6-13, 1924.

Scientific Sessions.

The following is the complete scientific program of the meeting:

PRESIDENTIAL ADDRESS.

Geologic factors in social evolution.....KIRTLEY F. MATHER

PUBLIC LECTURE.

How shall we measure the quantity of life?.....ALBERT P. MATHEWS

PAPERS.

1. Laboratory exercises in atomic structure. (15 min.),
WM. LLOYD EVANS AND JESSE E. DAY
2. The valley of ten thousand smokes in 1923. (20 min., lantern),
KIRTLEY F. MATHER
3. Tantalum: The newest metal contributed by science to industry. (30 min.),
JAMES R. WITHROW
4. Recent work in endocrinology. (30 min., lantern).....R. G. HOSKINS
5. The weather. (15 min.).....W. C. DEVEREAUX
6. Pressure and life. (15 min.).....STANLEY G. ZINKE
7. Glare: With demonstrations. (30 min.).....F. C. CALDWELL
8. Medical education in Colonial America. (15 min.).....F. C. WAITE
9. The relation of fish production to forestation. (10 min.),
RAYMOND C. OSBURN
10. The application of radio in distance determination. (20 min.),
GEORGE LEWIS
11. A hydrogen sulfide delivery system. (7 min.).....JESSE E. DAY
12. Respiration in the orthoptera. (15 min.).....M. O. LEE
13. The nutrition of *Euglena gracilis*. (10 min.).....W. J. KOSTER
14. Pest hunts in Wood County. (10 min.).....E. L. MOSELEY

15. The development of the intestinal coiling of the minnow (*Campostoma anomalum*). (10 min., lantern).....W. C. KRAATZ
16. Morphology of *gigantorhynchus* (*ancanthocephala*). (10 min.),
M. W. CASKEY
17. The periodical cicada in Ohio. (20 min., lantern).....H. A. GOSSARD
18. An Ohio record for the dragonfly (*Tachopteryx thoreyi*). (5 min.),
JAMES S. HINE
19. Parasites of the black bass. (10 min.).....R. V. BANGHAM
20. Habits of the common water snake, particularly in its relation to fish.
(5 min.).....F. A. HANAWALT
21. New terms suggested to designate the various modes of nutrition in
organisms. (5 min.).....W. J. KOSTIR
22. Recent mammal records in Ohio. (5 min.).....JAMES S. HINE
23. Ecologic notes on some homoptera of the southwest. (10 min., lantern),
HERBERT OSBORN
24. The early differentiation of the longitudinal zones in the neural plate of
rana. (10 min.).....R. A. KNOUFF
25. Two new hereditary tumors in *drosophila*. (15 min.).....IRA T. WILSON
26. The primitive lines in *amblystoma*. (15 min.).....F. L. LANDACRE
27. Comparisons of protozoan nuclei. (20 min.).....MAYNARD M. METCALF
28. A study of comparable developmental stages in chick and pig embryos.
(10 min.).....B. M. PATTEN
29. The differentiation of the epichordal and prechordal portions of the
brain in *amblystoma*. (10 min.).....R. C. BAKER
30. The spherical blackboard in the teaching of embryology. (5 min.),
EDWARD L. RICE
31. The effect on basal metabolism of ingested adrenalin chloride. (15 min.),
FRED A. HITCHCOCK
32. Heredity defects of the human hands, with special reference to symph-
alangism. (15 min.).....R. A. HEFNER
33. A novel type of symphalangism (?) or hypodactyly (?). (10 min.),
O. L. INMAN
34. Some practical and theoretical aspects of lubricating oil emulsions as a
scalecide. (10 min.).....L. L. HUBER
35. Interaction of the genes in the production of eye color in *drosophila*.
(10 min.).....W. P. SPENCER
36. The development of forestry practice. (25 min., lantern),
EDMUND SECREST
37. Botany: Opportunity. (15 min.).....MAXIMILIAN BRAAM
38. Present tendencies in high school biological courses. (10 min.),
WILLIAM E. NIEHAUS
39. Some Ohio inter morainal lakes and lake beds. (10 min., lantern),
GEORGE D. HUBBARD
40. The age of the glacial drift in Licking County, Ohio. (10 min.),
RALPH G. LUSK
41. Some glacial pebbles and cobbles found beyond the glacial boundary in
Muskingum and Guernsey counties. (10 min.).....C. F. MOSES
42. The composition of the Illinoian drift in Clermont County, Ohio. (5 min.),
G. W. CONREY
43. Drainage changes in the Warren-Youngstown-Sharon-New Castle areas.
(20 min.).....G. F. LAMB
44. Erosion levels in the Colorado Plateau. (15 min.).....ROBERT F. WEBB
45. Differences in the form of species usually regarded as common to North
America and Europe. (15 min.).....AUGUST F. FOERSTE
46. Plant life in ordovician and silurian times. (10 min.).....AUGUST F. FOERSTE
47. The positions occupied by orthoceroids while alive. (10 min.),
AUGUST F. FOERSTE
48. An amphibian trail from Pottsville formation. (5 min.).....G. F. LAMB
49. The Cleveland shale fishes of northern Ohio. (25 min., lantern). J. E. HYDE
50. Two recent papers on the earth's interior. (15 min.).....WALTER H. BUCHER

51. The importance of water conditions on the shallow oil sands of Ohio. (15 min.).....KENNETH COTTINGHAM
52. The structure of the Clinton sandstone in Ohio and its relation to oil and gas accumulation. (15 min.).....ROBERT LOCKETT
53. Clinton sand structure of northern Ohio in its relation to production. (15 min.).....A. W. MELHORN
54. A structural feature of Wood County, Ohio. (10 min.)....J. ERNEST CARMAN
55. The decline of mining activity in Colorado. (30 min., lantern),
FRANK R. VAN HORN
56. The glass sands of Ohio. (10 min.).....J. A. BOWNOCKER
57. Bacterial precipitation in fresh water. (15 min., lantern),
ALLYN C. SWINNERTON
58. The significance to sedimentation of the Amherst Berea deposits. (15 min., lantern).....J. E. HYDE
59. Some broader correlations of the Richmond. (15 min., lantern),
W. H. SHIDELER
60. The rock section at the O'Shaughnessy Dam. (10 min.)...J. ERNEST CARMAN
61. Effect of cutting upon the rate of hair growth. (5 min.)....R. J. SEYMOUR
62. Formation and structure of dental enamel. (15 min.)...SAMUEL W. CHASE
63. Status of the occupational disease question in Ohio, based on official figures. Present tendencies. (15 min., lantern)...EMERY R. HAYHURST
63. Recent studies on food accessories in a legume. (10 min.)...H. H. M. BOWMAN
64. Effect of basal metabolism of adrenalin by mouth. (10 min.),
F. A. HITCHCOCK
65. Factors that influence the knee jerk. (15 min.).....W. W. TUTTLE
66. Effect of adrenalin on the temperature of the brain. (10 min.),
W. P. SPENCER AND M. W. CASKEY
67. Relations of adrenals to bodily activities of the rat. (12 min.),
E. P. DURRANT
68. The effects of syphilis on dentition and on tooth structure. (15 min.),
L. J. KARNOSH
69. The nutritive value of a little-known bean. (10 min.)....H. H. M. BOWMAN
70. Blood sugar studies. (15 min.).....E. C. ALBRITTON
71. Calcium deficiency as a factor in psychopathy. (20 min.),
FLORENCE MATEER
72. Psychological method of studying. (30 min.).....HAROLD E. BURTT
73. A study in the evolution of concepts. (30 min.).....GARRY C. MYERS
74. Utilizing college records, including appointment blanks to predict after-college success of students. (15 min.).....LAURA CHASSEL TOOPS
75. An investigation of the development of personality in children. (10 min.),
O. R. CHAMBERS
76. Notes on musical aesthetics.....PAUL R. FARNESWORTH
77. The necessary postulates of empirical psychology. (15 min.), H. M. JOHNSON
78. The development of bisporangiate flowers in *Sagittaria latifolia*. (8 min.),
JOHN H. SCHAFFNER
79. A case of teratological inflorescence in alsike clover. (8 min.), FREDA DETMERS
80. Some new heritable characters of corn found in the culture at Ohio State University. Introduced by W. G. Stover. (10 min., lantern),
MARION T. MEYERS
81. Studies of variation in the fleshy fungi. (15 min.).....H. C. BEARDSLEE
82. The trend of investigation in plant growth. (20 min.).....H. C. SAMPSON
83. The change of opposite to alternate phyllotaxy in hemp by means of photoperiodism. (10 min.).....JOHN H. SCHAFFNER
84. The physiology of stomata. (20 min., lantern).....J. D. SAYRE
85. The diffusion of water-vapor through small openings. (20 min., lantern),
J. D. SAYRE
85. Water transfer in plant cells. (10 min.).....H. M. BENEDICT
86. The nutrition of *Euglena gracilis*. (10 min.).....W. J. KOSTIR
87. Some filamentous algae from Iowa. (10 min., lantern)....L. H. TIFFANY
88. The zygemaes. (15 min.).....E. N. TRANSEAU

89. The peculiar flora of the sand region west of Toledo. (10 min.),
E. L. MOSELEY
90. The distribution of the pine in Ohio. (20 min., lantern).....FOREST DEAN
91. The economic features of the yellow poplar in Ohio. (15 min., lantern),
O. A. ALDERMAN
92. Progress report on plantings on the slope of the dams in the Miami Conservancy District. (25 min., lantern).....A. E. WALLER
93. Observations of a plant collector on the Island of Hainan. (By invitation). Introduced by A. E. Waller. (30 min., lantern)...F. A. McCLURE
94. The uredinales of Ohio. (Preliminary). (10 min.).....W. G. STOVER
95. The relation of weather conditions to the development of apple scab at Columbus in 1923. (12 min., lantern).....HOWARD W. JOHNSON
96. The infection period of apple blotch in central Ohio in 1923. (8 min., lantern).....CURTIS MAY
97. The relation of *Fusarium moniliforme* to the ear, stalk and root-rot of corn. Introduced by W. G. Stover. (10 min., lantern)...D. P. LIMBER
98. Studies of toxin production in the fusarium wilt of tomato. Introduced by W. G. Stover. (10 min.).....IVAN E. MASSAR
99. A bud sport in *pelargonium* accompanied by the loss of two chromosomes. (Read by title).....PAUL B. SEARS

DEMONSTRATIONS.

- a. Yellow poplar wood.....O. A. ALDERMAN
- b. Corn.....MARION T. MYERS
- c. Lower jaw of a boar showing tusks.....WILLIAM E. NIEHAUS
- d. Water snake (*Tropidonotus fasciatus*) in the act of swallowing a creek sucker.....F. A. HANNAWALT
- e. Skeleton mount of common mole (*Scalopus aquaticus machrinus*). W. H. CAMP
- f. Plaster cast of earthworm (*Lumbricus terrestris*). Cross section,
HENRY OLSON
- g. Examples of certain homoptera of the Southwest, with photographs of their habitats.....HERBERT OSBORN
- h. Activity cages.....E. P. DURRANT
- i. The structure of dental enamel.....SAMUEL W. CHASE
- j. A novel form of symphalangism, or hypodactyly.....ONDESS L. INMAN
- k. A new type of physiographic map.....KIRTLEY F. MATHER

AN ANALYSIS OF THE CRANIAL GANGLIA OF AN EMBRYO SALAMANDER, AMBYSTOMA JEFFERSONIANUM (Green).

W. J. KOSTIR

*Department of Zoology and Entomology
Ohio State University*

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INTRODUCTION.

Since the pioneer work of Strong (1895) on the nerve components of the cranial nerves of Amphibia, a number of other papers have appeared dealing with the composition of these nerves in various members of the same group. Most of these studies have dealt with various species of urodeles, and have been concerned more particularly with the peripheral distribution of the nerves in the adult or late larval forms.

In these late larval and adult stages the ganglia of the cranial nerves are invariably more or less fused, forming in the Anura two, in the Urodela usually three, general ganglionic masses. In consequence of this fusion, the fundamental relations of the individual ganglia are largely obscured, and the analysis of these ganglionic masses into their component parts is made exceedingly difficult and oftentimes impossible.

The importance of studying early embryonic stages in which the fusion spoken of above has not yet taken place, and in which, therefore, the primary relations of the ganglia still obtain, was emphasized by Landacre and McLellan's analysis of the cranial ganglia of the embryo of *Rana* (1912). The present paper is offered as an attempt to analyze, by the use of similar methods, the cranial ganglia of an embryo urodele.

MATERIAL.

Except where otherwise stated, the descriptions, drawings, and reconstructions which follow are from a single embryo of *Ambystoma jeffersonianum* (Green), 11.5 mm. in length. This embryo was killed about nineteen days after fertilization, most of the development having taken place in a room where the temperature was mild and fairly constant. Most of the remaining embryos of the same egg mass hatched six days later. A considerable number of other specimens, some younger and some older than the 11.5 mm. embryo, were also studied and the conclusions reached from the study of the latter were thus checked up.

It was found that considerable variation in position and in degree of fusion between the ganglia was present in embryos of approximately the same age. Even the two sides of the same individual often presented considerable differences. Nevertheless, the more general relations between the ganglia and between these and their roots and rami were found, on the whole, to remain constant. Likewise, while the degree of fusion between given parts might be considerably less in some older individuals than in certain younger ones, there was found to obtain in general a definite progression from the free to the fused condition paralleling the progression from early to late stages. The 11.5 mm. embryo described was selected because it showed what seemed to be, on the whole, the most typical condition for that stage.

The material was killed and fixed in Zenker's fluid, and after sectioning was stained with Delafield's hæmatoxylin and orange G. The studies were made almost entirely from transverse sections 10 microns in thickness, though two specimens cut into parasagittal sections of the same thickness were also used.

For this material, and for numerous suggestions and criticisms as well, I wish to acknowledge my deep obligation to Professor F. L. Landacre.

SCOPE AND METHODS.

While the cranial ganglia in the 11.5 mm. embryo are more crowded together than in earlier stages, and a certain amount of fusion has already taken place, this embryo was chosen for

detailed study and reconstruction because of the much more complete development of the nerve trunks and their branches. This made possible certain identification of the various ganglia, which was the main object of the present investigation. However, a detailed study of the distribution of the nerves was not attempted; and only as much of this distribution is given in the following description as seems necessary to establish the character of the several ganglia. For the sake of clearness and simplicity, the distribution of the nerves is not included in the reconstruction. For the same reason, while all motor components that were definitely identified as such are described in the text, these have been omitted from the reconstruction.

The lateral view reconstruction shown in Plate I was made by the ordinary method of projecting, by means of a camera lucida, sections magnified to a definite size upon coordinate paper, and plotting the upper and lower limits of the various structures in consecutive sections. The reconstruction is thus a projection of these structures upon the sagittal plane.

The nomenclature used has been, as far as possible, the same as that of Coghill (1902), whose thorough and painstaking description of the cranial nerves in the late larval stage of *Ambystoma tigrinum* was found of great assistance. To some extent, however, I have made use of the nomenclature of Landacre and other authors.

GENERAL STATE OF DEVELOPMENT OF THE 11.5 MM. EMBRYO.

In the 11.5 mm. embryo of *Ambystoma jeffersonianum* the general relations of the parts of the central nervous system are already essentially the same as in the adult, though the brain is comparatively shorter antero-posteriorly, and the cephalic flexure is more marked. The cranial ganglia are readily recognizable, and their roots and principal trunks and rami are for the most part well defined. In the preparations studied no trace of myelination of the fibers can as yet be detected; though usually numbers of elongated cells (the future sheath-cells) are strung along the bundles of fibers. A root or ramus when cut in cross-section often shows the nuclei of some of these cells in among the fibers. In many cases fibers can be traced directly to the muscles, sense-organs, or other tissues which they innervate; but for the most part this is very difficult, owing to the

absence of myelination and the obscuring presence of numerous yolk-laden mesenchyme cells.

At this stage of development the differences in size and staining reaction between the fibers of different components, reported by various writers, are not observable; except that when, as is rarely the case, isolated fibers are found, those from lateralis ganglia appear to be slightly larger than those from other ganglia.

The auditory vesicle, in the embryo here described, is in an early stage of the formation of the semi-circular canals; the septa of the lateral and anterior canals have just been formed, while that of the posterior canal is represented as yet only by an infolding of the lateral wall of the vesicle, which fold projects mesio-ventrad into the cavity of the latter. (Norris, 1892).

Lateral line organs are numerous on the side of the head, and readily recognized.

The skeletal system is in a very early stage of development. The chondrocranium is as yet represented only by the parachordals and the trabeculae, which at this time are little more than narrow bars. The visceral arches (branchial bars) are fairly well defined. The palatoquadrate cartilages are not as yet fused with the trabeculae. All these structures are in a very early stage of chondrification. Actual chondrification of the auditory capsule has not as yet commenced, though an organization of mesenchyme about the vesicle, preparatory to chondrification, is already apparent.

The pharynx is still closed anteriorly at this stage. Gill clefts have not yet appeared, but their future position is indicated by endodermic outgrowths from the wall of the pharynx to the spaces between the external gills. The breaking open of the mouth and that of the gill clefts seem to take place nearly at the same time, and but little later than the stage described.

THE GANGLIA OF THE V (TRIGEMINUS), VII (FACIALIS), AND VIII (AUDITORY) NERVES.

The ganglia of the V, VII, and VIII nerves fall distinctly into two groups. The Gasserian and dorsal lateralis VII ganglia comprise the more anterior group; the geniculate, ventral lateralis VII, and auditory ganglia comprise the more posterior. This grouping is not, however, as striking a feature as it seems

to be in some of the late larval forms hitherto described, the anterior border of the geniculate ganglion, for example, being barely 10 microns posterior to the most posterior portion of the Gasserian (Plate I). Later in the development (in the young larva) the lengthening of the head brings with it an increase in the distance between these ganglia; and the work of Coghill (1902) shows that this tendency becomes even more marked in the late larval stages.

Cutaneous V or Gasserian Ganglion.

The Gasserian ganglion, at this stage, is readily recognized as a rather large mass of cells, somewhat oblong in cross-section, and pressed close to the lower portion of the side of the medulla at the anterior end of the latter (Plate I, *G. Gass. + Prof.*; Plate II, Fig. 1, *G. Gass.*; Plate IV, Fig. 1a). Its anterior portion extends for a short distance into the region between the brain and the optic vesicle; its posterior part for a shorter distance into that between the brain and the auditory vesicle. Its ventro-lateral portion is in contact with the anterior extremity of the palatoquadrate bar (Plate II, Fig. 1; Plate IV, Fig. 1a).

At this stage no distinction can be made out with certainty between the profundus portion and the Gasserian proper portion of the ganglion. In considerably earlier stages, however, this distinction is very marked, the profundus portion projecting forward for a considerable distance above the optic vesicle. In these earlier stages both portions of the ganglion lie much closer to the ectoderm of the side of the head.

In its posterior part the dorsal portion of the Gasserian ganglion is in close contact with the dorsal lateralis VII ganglion (Plate I, and Plate II, Fig. 1, *G. D. L. VII*). The two are readily separated, however, because of the histological differences between them. (See p. 251; also Plate IV, Fig. 1a).

The root of the Gasserian ganglion leaves its dorso-mesial surface near the center of its posterior half. (See Plate I, dotted lines, and Plate II, Fig. 1, *Rt. Gass.*; also Plate IV, Fig. 1a). It is exceedingly short, entering the medulla at a point directly opposite its point of exit from the ganglion. In older stages the root becomes considerably longer, and runs caudad for some distance before entering the medulla; this is the condition which has been uniformly reported for late larval stages in urodeles.

Three rami arise from the Gasserian ganglion. The *ramus ophthalmicus profundus V* (Plate I, *R. O. P. V*) arises from its most anterior portion; it dips at first rather suddenly downward for a short distance, and then takes its course forward between the brain and the optic vesicle.

The *ramus maxillaris V* (Plate I, *R. Mx. V*) arises from the dorso-lateral part of the ganglion, at a transverse level nearly at the middle of the ganglion. It at once unites with the *ramus buccalis VII* to form the infra-orbital trunk, which takes its course at first latero-ventrad and a little forward, and then more directly forward between the optic vesicle and the skin, close to the outer surface of the former.

The *ramus mandibularis V* (Plate I; Plate II, Fig. 1; Plate IV, Fig. 1a; *R. Mnd. V*) leaves the lateral portion of the ganglion a few sections posterior to the origin of the *ramus maxillaris*, and at a point directly dorsal to the palatoquadrate bar. It runs at first latero-ventrad and then almost directly ventrad between the temporalis and masseter muscles to the region of Meckel's cartilage. The further course of its principal portion is in general cephalad. Fibers from it were traced directly to the undifferentiated ectoderm, below Meckel's cartilage, helping thus to confirm the general cutaneous character of the ganglion.

Motor component V. In the postero-ventral portion of the root of the Gasserian, a bundle of fibers may be recognized as a motor component because of the fact that its fibers, unlike the rest, after entering the medulla run down into its ventral horn. These fibers pass directly through the ganglion, emerging with and as a part of the *ramus mandibularis*, in which they occupy a postero-ventral position. A short distance beyond the ganglion a portion (at least) of these fibers is given off from the ventral side of the *ramus mandibularis*, and innervates the temporalis muscle, thus confirming the motor character of this component.

Dorsal Lateralis VII Ganglion.

Throughout most of its length this ganglion appears in cross-section as a more or less rounded or oblong mass dorsal to the Gasserian, to which for some distance it is closely pressed (Plate I; Plate II, Fig. 1; Plate IV, Fig. 1a; *G. D. L. VII*). Nevertheless, as stated above, the two can be readily distin-

guished. Its posterior portion extends backward between the auditory vesicle and the medulla, and gives rise to its root at a transverse level but little farther caudad than that of the posterior end of the Gasserian. This root, owing to the narrow space between the ear and the medulla through which it passes, is much compressed from side to side, giving it, in the reconstruction, a false appearance of great bulk (Plate I, *Rt. D. L. VII*). The root continues backward to its junction with the root of the ventral lateralis VII ganglion (Plate I; Plate II, Fig. 2; Plate IV, Fig. 2a). Slightly posterior to this junction the combined roots enter the medulla. This point of entrance is at a horizontal level much higher than that of the root of the Gasserian. (Plate I, dotted lines; also Plate II, Fig. 3, *Rt. D. + V. L. VII*).

The *ramus ophthalmicus superficialis VII* (Plate I, *R. O. S. VII*) leaves the dorsal lateralis VII ganglion at its anterior end. It passes forward and somewhat dorso-laterad for a considerable distance, running directly above the eye. Branches from it were traced to the lateral line organs of this region. No evidence was found of any other component in this ramus.

About four sections (40 microns) farther back the *ramus buccalis VII* (Plate I, *R. Bu. VII*) leaves the ventro-lateral portion of the ganglion, and at once joins with the cutaneous ramus maxillaris V to form the infra-orbital trunk. At the point where the two unite, a branch is given off posteriorly (Plate I; Plate II, Fig. 1; Plate IV, Fig. 1a; *R. Bu. VII, 1*) which runs ventro-laterad and for a short distance back around the anterior end of the auditory vesicle. Its fibers were traced to lateral line organs in this region. The general course of the main portion of the infra-orbital trunk has been given above (p. 235). Fibers from it were traced to numerous lateral line organs.

Ventral Lateralis VII Ganglion.

This, the farthest ventrally of all the ganglia here described, is a spindle-shaped mass of cells lying ventral to the anterior portion of the auditory vesicle (Plate I; Plate II, Figs. 2 and 3; Plate IV, Figs. 2a and 3a; *G. V. L. VII*). Its long axis is directed ventro-laterad and slightly caudad. Its proximal end is well fused with the distal portion of the geniculate ganglion, although, as in the case of the dorsal lateralis VII and Gasserian

ganglia, the boundary between the two is readily recognized. The distal end of the ganglion lies upon and in contact with an outgrowth of endoderm which projects dorsad from the lateral angle of the pharynx in this region (Plate II, Figs. 2 and 3; *En.*).

The root of the ventral lateralis VII ganglion is comparatively long (Plate I; Plate II, Fig. 2; Plate IV, Fig. 2a; *Rt. V. L. VII*); as it runs mesio-dorsad to its junction with the root of the dorsal lateralis ganglion, it is pressed between the geniculate ganglion, the auditory vesicle, and the anterior border of the auditory ganglion.

But one ramus arises from this ganglion, the *ramus mentalis VII* (Plate I; Plate II, Fig. 3; Plate IV, Fig. 3a; *R. Mnt. VII*). This component of the hyomandibular trunk leaves the distal extremity of the ganglion; it passes, just posterior to the articulation of Meckel's cartilage with the palatoquadrate bar, abruptly ventrad and lateral to the hyoid bar. When close to the ectoderm in the ventro-lateral region of the head it turns forward, supplying lateral line organs in this region and farther cephalad. A short distance from the ganglion it gives off a lateral branch which passes directly to the skin and likewise innervates lateral line organs.

Visceral VII or Geniculate Ganglion.

The geniculate ganglion (Plate I; Plate II, Figs. 2 and 3; Plate IV, Figs. 2a and 3a; *G. Gen.*) is directly posterior to the Gasserian, and in the 11.5 mm. embryo it almost touches the posterior border of the latter. In its anterior portion it is roughly wedge-shaped as seen in cross-section, the point of the wedge extending dorsad between the medulla and the ear (Plate II, Fig. 2; Plate IV, Fig. 2a). Posteriorly the ganglion is pressed close against the antero-mesial surface of the auditory ganglion, the anterior end of which is introduced between the geniculate ganglion and the ear (Plate II, Fig. 3; Plate IV, Fig. 3a; *G. Aud.*). This contact between the two ganglia is very close, and in some specimens it is very difficult to distinguish the exact boundary between the two.

The root of the geniculate ganglion (Plate I; Plate II, Fig. 3; Plate IV, Fig. 3a; *Rt. Gen.*) arises from its postero-dorsal portion; it passes dorsad and caudad for a short distance, pressed close to the mesial surface of the auditory ganglion, and enters the medulla at a horizontal level lower than the

lateralis root of VII, yet somewhat higher than the root of the Gasserian. The area of entry is but two or three sections (20 or 30 microns) farther caudad than that of the lateralis root.

Two rami arise from the geniculate ganglion. The *ramus alveolaris VII*, the visceral component of the hyomandibular trunk, leaves the ventro-lateral portion of the ganglion, directly underneath the proximal end of the ventral lateralis VII ganglion (Plate I, *R. Alv. VII*). It proceeds parallel to the long axis of this latter ganglion, in close contact with its ventral surface (Plate II, Fig. 3; Plate IV, Fig. 3a), and soon turns abruptly ventrad, running parallel and mesial to the *ramus mentalis*, but quite distinct from it. At about the horizontal level of the middle of the pharynx it turns forward and runs cephalad. When traced forward it is soon lost, its fibers apparently ending in the epithelium of the pharynx.

The *ramus palatinus VII* (Plate I, *R. Pal. VII*) leaves the antero-ventral portion of the ganglion and inclines cephalo-ventrad. Its fibers also end in close relationship with the epithelium of the pharynx.

Auditory Ganglion.

The auditory ganglion (Plate I; Plate II, Figs. 3 and 4; Plate IV, Figs. 3a and 4a; *G. Aud.*) lies between the ventral portion of the auditory vesicle and the medulla, and throughout most of its length is in contact with the former. Its anterior portion is wedged in between the ear and the geniculate ganglion (Plate II, Fig. 3; Plate IV, Fig. 3a), and its anterior-most border is in contact with the root of the ventral lateralis VII ganglion. Its dorso-ventral extent is much greater anteriorly than farther back, reaching from a level below the base of the medulla to a level just above the area of entry of the root of the geniculate. Posteriorly it tapers, somewhat more rapidly on its upper surface, and reaches as far as the posterior third of the auditory vesicle.

The only root of the auditory ganglion recognized with certainty as such leaves its dorso-mesial portion, and, passing slightly caudad and dorsad, enters the medulla in contact with and ventro-posterior to the root of the geniculate (Plate I, *Rt. Aud.*). It is in even closer relationship with the motor root which leaves the medulla just ventral to it; the exact limits of these roots are very hard to distinguish.

Coghill describes two auditory ganglia, a vestibular and a cochlear, each with its own root, in the late larval stage of *Ambystoma*. Norris finds two auditory roots in *Amphiuma*, but does not distinguish two distinct ganglia, merely recognizing vestibular and cochlear portions of one auditory ganglion. In the embryo here described it has likewise been impossible to distinguish two distinct ganglia. In young larval stages considerably older than the 11.5 mm. embryo, two different regions, one more anterior and dorsal, the other more posterior and ventral, may be identified. These regions are characterized by histological differences (p. 252), but no definite boundary between them can be determined. In the 11.5 mm. embryo the beginnings of this histological differentiation can be just barely recognized, and the transition in structure from one portion of the ganglion to the other is even more gradual than in later stages.

Only two rami from the auditory ganglion, both of them small and unbranched, are present in the 11.5 mm. embryo. The larger and more anterior of these (Plate II, Fig. 3; Plate IV, Fig. 3a; *R. Utr. VIII*; not shown in reconstruction) arises from the ventro-lateral portion of the ganglion, near its anterior end, and passes laterad in close contact with the ventral surface of the auditory vesicle to the macula of the utricle; a few of the fibers appear to pass beyond to the crista of the horizontal canal. The smaller and more posterior ramus (Plate II, Fig. 4; Plate IV, Fig. 4a; *R. Sac. VIII*; not shown in reconstruction) arises from the postero-lateral portion of the ganglion and passes laterad to the macula of the sacculus. These small rami are undoubtedly the incipient *ramus acusticus utriculi* and *ramus acusticus sacculi* respectively.

Motor component VII. Immediately ventral to the area of entry of the auditory root a bundle of motor fibers emerges from the medulla. The character of this component is indicated by the course of the fibers within the medulla, where they are readily traced to the ventral horn, and is confirmed by their peripheral distribution. The component extends ventro-laterad, pressed close between the auditory and geniculate ganglia (Plate II, Fig. 3; Plate IV, Fig. 3a), and as it emerges from between them it comes to lie on the posterior surface of the ventral lateralis ganglion. Thence it continues ventro-laterad for a short distance, and its fibers enter the depressor mandibulae muscle. At all points its fibers are quite distinct from those of the remainder of the hyomandibular trunk.

THE GANGLIA OF THE IX (GLOSSOPHARYNGEUS) AND X (VAGUS) NERVES.

At the stage of the 11.5 mm. embryo the ganglia of the IX-X complex are in a condition intermediate between the earliest stage of well-defined and almost entirely separate ganglia and the later stage of complete fusion into one ganglionic mass. The ganglia are already crowded together, and to some extent actual fusion has taken place. For the most part, however, the limits of the individual ganglia are readily discernible.

In the more general relations of its parts this group bears a distinct resemblance to the same complex in the embryo of *Rana*, as reported by Landacre and McLellan. The visceral ganglia—visceral IX, or petrosal, and visceral X, or nodosal—are ventral in position; the one cutaneous ganglion—cutaneous X, or jugular—more dorsal and mesial; while the lateralis ganglia, present, as in *Rana*, in both IX and X, occupy a position dorsal and lateral to the other ganglia of the complex.

The roots of these ganglia enter the medulla in three distinct areas. Of these, the most anterior is that of the one lateralis root of the complex, composed of all the lateralis root fibers from both IX and X. Slightly caudad and ventrad of this enters the root of the visceral IX ganglion; and considerably farther back the roots of the visceral X and cutaneous X ganglia enter together.

These relations are essentially the same as those described by Coghill for the late larval stage of *Ambystoma*, except that he describes two roots for visceral X, entering the medulla separately. This I have not been able to demonstrate in the 11.5 mm. embryo, nor in any of the other stages at hand. All the visceral root fibers from X apparently enter the medulla together.

Visceral IX or Petrosal Ganglion.

The most anterior of the ganglia of the IX-X complex is the visceral IX (*G. petrosum*). (Plate I; Plate III, Figs. 5, 6, and 7; Plate IV, Figs. 5a, 6a, and 7a; *G. Vi. IX*). It lies immediately posterior to the auditory vesicle, its dorso-anterior portion extending mesial to the posterior extremity of the latter. In cross-section it is more or less oval in shape, and the long axis is inclined ventro-laterad.

The root of the visceral IX ganglion (Plate I, *Rt. Vi. IX*) arises from its antero-dorsal portion, and passes forward and mesio-dorsad for about eight sections (80 microns) before entering the medulla. The area of entry is ventro-posterior to that of the lateralis IX and X root; its horizontal level (with respect to the base of the medulla) is nearly the same as that of the root of the geniculate ganglion. Motor fibers were recognized in this root, in the same way as in the roots of V and VII, but I was not able to trace them through the ganglion.

The one nerve that leaves this ganglion, the *truncus glossopharyngeus IX* (Plate I; Plate III, Fig. 5; Plate IV, Fig. 5a; *T. Gl. IX*), arises from its ventro-lateral border and passes ventro-laterad and slightly cephalad to the region of the first branchial bar. A short distance beyond the ganglion a small branch (not shown in the reconstruction) is given off ventrally, and passes ventro-cephalad. It could not be traced very far, but apparently ends while in close relationship with the epithelium of the pharynx.

Just above the first branchial bar the glossopharyngeal trunk passes close to the first levator arcus branchialis muscle, and a portion of its fibers (motor component of IX) enter this muscle. The principal portion of the trunk turns cephalad, and extends in this general direction for a long distance, at first lateral to the first branchial bar, but gradually passing ventrad and mesiad; it finally ends in the epithelium of the basal portion of the tongue. It should be noted here that this is not the complete distribution of the glossopharyngeal trunk. As in the case of other trunks and rami, minor branches were not followed.

The *ramus communicans IX + X ad VII*, described by Coghill, Bowers, and Norris as present in the late larval stages of *Ambystoma*, *Spelerpes*, and *Amphiuma* respectively, could not be found in any of the embryos or young larvæ which I studied.

Coghill finds in the late larva of *Ambystoma* a cutaneous component in the *truncus glossopharyngeus*, apparently derived from the cutaneous X ganglion. This, again, I was not able to demonstrate in the material at hand.

Lateralis IX and X Root.

Before taking up any of the lateralis ganglia of IX and X, a few words regarding the common root of these ganglia (Plate I,

Rt. L. IX + X) will prove helpful. The most posterior portion of this root arises from the dorsal lateralis X ganglion (Plate I, *G. D. L. X*), well back in the complex, and extends cephalad, for most of the distance dorsal to the cutaneous X ganglion (Plate III, Figs. 6, 7, and 8; Plate IV, Figs. 6a, 7a, and 8a; *Rt. L. X*; *G. Cu. X*) as far as the lateralis IX ganglia (Plate I; Plate III, Figs. 5 and 6; Plate IV, Figs. 5a and 6a; *G. D. L. IX* and *G. V. L. IX*). As it passes close to the mesial surface of the latter, the root fibers of these ganglia are added to it. Running dorsal to the visceral IX root, it continues cephalad, and now somewhat dorso-mesial, to its area of entry into the medulla. This area is antero-dorsal to that of the visceral IX root, and is nearly at the same horizontal level as that of the lateralis roots of VII.

On one side of one individual, a radical variation was found, the lateralis root of X entering the medulla quite separate from that of IX, and a short distance farther caudad than the lateralis and visceral roots of IX. What significance, if any, this interesting variation may have, it is impossible to say; the mere possibility that it is a reversion to a more primitive condition naturally suggests itself.

Lateralis IX Ganglia.

In the earlier stages there are two distinct lateralis ganglia present in close relationship with the visceral IX ganglion. Each sends its own root to join the general lateralis root of IX and X. From the more anterior and ventral of these ganglia the ramus supratemporalis IX arises; from the more posterior and dorsal, the lateralis component of the ramus auricularis IX + X. These two ganglia usually soon fuse, to a greater or less degree, and in the 11.5 mm. embryo they appear as one continuous ganglion. (Plate I; Plate III, Figs. 5 and 6; Plate IV, Figs. 5a and 6a; *G. D. L. IX* and *G. V. L. IX*). The apparent bilobing of this ganglion in the reconstruction does not accurately represent this double condition, though roughly it does; the more ventral of the ganglia is represented by a portion of the upper lobe as well as all of the lower.

In some individuals of stages somewhat older than the 11.5 mm. embryo, and even in a few of that stage, the dorsal lateralis IX ganglion comes into close contact with the ventral lateralis X ganglion, forming with it a single, continuous mass of cells.

From a study of such cases alone it would be easy to infer that the two actually represent but a single ganglion, and that the lateralis component of the R. auricularis therefore arises from ventral lateralis X. Against this interpretation, however, must be placed the indisputable fact that the cell masses which form these two ganglia are uniformly quite distinct in the early stages, and in the greater number of cases remain distinct for a considerable time, even after the development of the nerves to which they give rise.

Because of the close relationship of both dorsal and ventral lateralis IX to the visceral IX ganglion, and because of their usual fusion with each other, it seemed best to place both these ganglia on IX. However, it seems quite possible that the ganglion identified as dorsal lateralis IX actually belongs primitively on X, and corresponds to the first of the three lateralis ganglia on X which Landacre has described in *Squalus*. Either interpretation is bound to be more or less arbitrary.

In the 11.5 mm. embryo the greater part of the combined lateralis IX ganglia lies directly above the visceral IX ganglion, and in contact with the lateral border of the lateralis IX and X root (Plate III, Fig. 5; Plate IV, Fig. 5a). The individual roots of both lateralis IX ganglia can be distinguished, though with great difficulty, as both are exceedingly short before they unite with the root of lateralis X.

The combined lateralis IX ganglia comprise a comparatively small mass of cells; the most ventral portion, as seen in transverse section, consists merely of a single or at most a double layer of cells pressed close to the dorso-lateral border of the visceral IX ganglion. The appearance of this ventral portion in the reconstruction is deceptive, its size as seen in the lateral view giving the idea of considerable bulk, which it does not possess. (Compare Plate I with Plate III, Figs. 5 and 6.) The cells of this ventral portion extend down toward the point of origin of the truncus glossopharyngeus, and in some specimens strongly suggest the idea that they may send lateralis fibers into this trunk. However, no such fibers could be traced with certainty; and as far as the distribution of the glossopharyngeal trunk was followed, no lateral line organs could be found to be innervated by its fibers.

The actual number of rami from lateralis IX seems to vary somewhat with the age. In the 11.5 mm. embryo there are three

definite rami (Plate I; Plate III, Figs. 5 and 6; Plate IV, Figs. 5a and 6a; *R. Spt. IX*; and *R. Aur. 1, IX* and *R. Aur. 2, IX*) and one slight fibrous outgrowth which does not as yet extend far beyond the surface of the ganglion (Plate III, Fig. 5; Plate IV, Fig. 5a; *R. Aur. ?*, not shown in the reconstruction). A study of many individuals of various stages shows that these rami fall distinctly into two groups, each group arising from a different one of the two original ganglia of which lateralis IX is composed. The distribution of these two groups corresponds in a general way with that usually given for the ramus supratemporalis and ramus auricularis respectively. Moreover, the more posterior of these groups is almost invariably closely associated near its place of origin with a component from the cutaneous X ganglion, while the other is not. As this also agrees with the conditions of the two rami as reported in late larval stages of both *Ambystoma* and *Amphiuma*, there seems to be no doubt of the homology.

In the 11.5 mm. embryo the *ramus supratemporalis IX* (Plate I; Plate III, Fig. 5; Plate IV, Fig. 5a; *R. Spt. IX*) arises from the antero-lateral portion of the combined lateralis IX ganglia. It passes laterad and somewhat dorso-cephalad around the hind border of the auditory vesicle and innervates lateral line organs in the region of the posterior portion of the ear. Its subdivisions seem to vary in different individuals, but in most it shows two main branches, one more dorsal than the other.

The two rami which I have identified as lateralis components of the *ramus auricularis IX + X* (Plate I; Plate III, Fig. 6; Plate IV, Fig. 6a; *R. Aur. 1, IX* and *R. Aur. 2, IX + X*) arise from the dorso-lateral portion of the combined ganglia, a little farther caudad and considerably farther dorsad than the origin of the ramus supratemporalis. They arise together, the more anterior (*R. Aur. 1*) extending dorso-laterad and then a little cephalad. The other (*R. Aur. 2*) inclines more caudad; it unites at once upon leaving the ganglion with fibers from the cutaneous X ganglion, and runs latero-dorsad, and for a short distance caudad, to the ectoderm. Fibers from both these rami were traced to lateral line organs in the region just posterior to the ear.

Cutaneous X or Jugular Ganglion.

Of the four ganglia of X, the cutaneous X or jugular ganglion (Plate I, *Rt. G. Cu. X*; Plate III, Figs. 6, 7, and 8; Plate IV,

Figs. 6a, 7a, and 8a; *G. Cu. X*) is closest to the wall of the medulla. It also extends the farthest forward, its anterior portion projecting cephalo-laterad between the dorsal lateralis IX, above, and ventral lateralis IX, together with visceral IX, below. (See Plate III, Fig. 6; Plate IV, Fig. 6a.)

As was stated above, the lateralis X root passes cephalad close to the dorsal surface of the cutaneous X ganglion; a small portion of the ganglion extends slightly dorso-mesial to this root (Plate III, Figs. 6 and 7; Plate IV, Figs. 6a and 7a). Lateral to the cutaneous ganglion lie the anterior portions of the ventral lateralis X and visceral X ganglia, the visceral X being crowded close against most of the lower portion of its lateral border (Plate III, Figs. 7 and 8; Plate IV, Figs. 7a and 8a). The limits of the two ganglia, are, nevertheless, readily distinguished.

The root of the cutaneous X ganglion (Plate I, *Rt. G. Cu. X*; Plate III, Figs. 6 and 7; Plate IV, Figs. 6a and 7a; *Rt. Cu. X*) arises from its dorso-mesial portion; it passes dorso-mesiad, in company with the root of the visceral X ganglion and a portion of the motor fibers of X, directly to the medulla. This combined cutaneous, visceral, and motor root is very thick. The horizontal level of its area of entry into the medulla, with reference to the base of the medulla, is somewhat lower than that of the Gasserian or geniculate roots; but since the height of the medulla at this point is considerably less than in the region of V and VII, relatively the level is approximately the same.

The only ramus from this ganglion that could be identified with certainty as such was the cutaneous component of the *ramus auricularis IX + X* (Plate I; Plate III, Fig. 6; Plate IV, Fig. 6a; *R. Aur. 2, IX + X*). This arises from the most anterior and lateral portion of the ganglion, just ventral to the posterior portion of the dorsal lateralis IX ganglion, and at once joins with the lateralis component from the latter. The two pass dorso-laterad and somewhat caudad to the ectoderm of the region just posterior to the ear. Some of the fibers were traced to undifferentiated ectoderm, confirming the cutaneous character of this component.

The cutaneous components found by Coghill in the glosso-pharyngeal trunk and in both branchial trunks in the late larval stage of *Ambystoma*, I was not able to demonstrate with certainty in my material.

Visceral X or Nodosal Ganglion.

In the earlier stages the visceral X ganglion (*G. nodosum*) (Plate I; Plate III, Figs. 7, 8, and 9; Plate IV, Figs. 7a, 8a, and 9a; *G. Vi. X*) shows a very evident division into two parts, the more anterior of these giving rise to the two branchial trunks, the posterior to the visceral trunk. The two portions are continuous with each other, the division between them being marked simply by a very decided constriction in the middle portion of the ganglion.

This division of the visceral X ganglion into two parts, a branchial and a visceral, was also found by Landacre and McLellan in the embryo of *Rana*. The possible homology of the anterior portion with one or more of the branchial ganglia of fishes is discussed by these authors. A comparison with the visceral ganglia of X in *Menidia* (Herrick, 1899) or *Squalus* (Landacre, 1916) strongly suggests the probability of such a homology.

In the 11.5 mm. embryo from which the reconstruction was made, the constriction between the two portions of the visceral X ganglion has disappeared, and the ganglion appears as a single large, elongated mass, which is somewhat larger in transverse extent in the region of the branchial trunks than farther back. In some specimens, however, this constriction persists to a much later stage of development.

Anteriorly the visceral X ganglion extends, together with the ventral lateralis ganglion just above it, for a slight distance latero-dorsal of the visceral IX ganglion. Its anterior third is in close contact with the lower portion of the lateral surface of the jugular ganglion. Throughout most of its extent, the lateralis X ganglia lie in close contact with its dorsal, and to some extent lateral, surfaces, as will be described below.

The root of the visceral X ganglion (Plate I; Plate III, Figs. 6, 7, and 8; Plate IV, Figs. 6a, 7a, and 8a; *Rt. Vi. X*) leaves its dorso-mesial surface, a little caudad of the posterior border of the cutaneous ganglion. It passes, at first pressed close to the posterior surface of the latter ganglion, dorso-mesial and somewhat cephalad to the medulla, which it enters in company with the cutaneous root and a portion of the motor root of X.

The visceral components of the two *branchial trunks* (Plate I; Plate III, Fig. 8; Plate IV, Fig. 8a; *T. Br. 1, X* and *T. Br. 2, X*) leave the ganglion close together. They arise from its ventro-lateral border, not far from its anterior end, the place of origin of the second branchial trunk being usually just posterior to that of the first. The course of the first of these is in general ventro-laterad and somewhat caudad; that of the second is similar, but more caudad.

A short distance beyond the ganglion a ventral branch (not shown in the reconstruction) leaves the first branchial trunk; it inclines ventro-caudad and soon disappears in contact with the epithelium of the pharynx. This is evidently the "pharyngeal ramus, 1 br. 1," of Coghill (1902, Plate XVI).

On their way to the periphery, both branchial trunks come into close relations with certain small gill muscles (not identified); and it appears quite probable that motor fibers present in these trunks are given off to these muscles, as Coghill found to be the case in the late larval stage. This could not be demonstrated, however, in the 11.5 mm. embryo. The greater portion of the fibers of these trunks passes to the region of the three external gills.

The *truncus visceralis X* (Plate I, *T. Vi. X*) leaves the posterior extremity of the visceral X ganglion and extends ventro-caudad. A very short distance beyond the ganglion a lateral branch (Plate I, *T. Vi. X. 1*) leaves the trunk and extends latero-caudad to the region of the third external gill. The main portion of the trunk continues ventro-caudad and comes into close relations with the alimentary canal in the region posterior to the gills. A portion at least of its fibers may be traced to the epithelium of the alimentary canal in this region.

Dorsal Lateralis X Ganglion.

This ganglion (Plate I, *G. D. L. X*) lies throughout its whole extent dorsal to the visceral X, and posteriorly becomes in some individuals partially fused with it (Plate III, Fig. 9; Plate IV, Fig. 9a). Its anterior end is at about the transverse level of the visceral X root; its posterior end about as far caudad as the posterior end of the visceral ganglion. In early stages it is quite separate from the ventral lateralis X, but in the 11.5 mm. embryo the latter has become fused with a portion of its ventro-lateral border. (Plate III, Fig. 9; Plate IV, Fig. 9a).

The root of the dorsal lateralis X ganglion has been described above as the most posterior portion of the lateralis IX and X root. (See pp. 241 and 242).

But one ramus leaves the dorsal lateralis X ganglion, the *ramus lateralis superior X* (Plate I, *R. L. s. X*), which is purely lateralis in character. It arises from the posterior extremity of the ganglion and extends directly caudad. A short distance beyond the ganglion a branch is given off dorsally (Plate I, *R. L. s. d. X*), which after ascending a little continues caudad more or less parallel with the main portion of the ramus. Both portions supply lateral line organs along the dorsal portion of the side of the body.

Ventral Lateralis X Ganglion.

Up to the present time two lateralis ganglia on X have been definitely described for Amphibia only by Landacre and McLellan in the embryo of *Rana*. The more general relations of the ventral lateralis X ganglion in that form are almost exactly the same as those of the ganglion to which I have given that name in the embryo of *Ambystoma*. (Plate I; Plate III, Figs. 7, 8, and 9; Plate IV, Figs. 7a, 8a, and 9a; *G. V. L. X*).

In all the stages studied, this ganglion lies in contact with the dorso-lateral surface of the visceral X ganglion; and this contact is maintained usually throughout its whole length. In the later stages studied it is usually fused more or less completely with the dorsal lateralis IX ganglion and the ventral border of the dorsal lateralis X. In early stages, however, it is uniformly quite distinct from both of these. In the 11.5 mm. embryo from which the reconstruction was made, the process of fusion had gone farther on one side of the body than on the other. On the right side, which was plotted, the ventral lateralis X ganglion, while close to lateralis IX, was quite separate from it; on the left side the two had come into contact, though the limits of each were still recognizable. On both sides of the body the dorsal and ventral lateralis X ganglia were already partly fused. (Plate I; Plate III, Fig. 9; Plate IV, Fig. 9a).

In its anterior portion the ventral lateralis X ganglion extends much farther dorsad than it does farther back, its dorsal border rising to the level of the root of the dorsal lateralis X ganglion, and lying just lateral to it. (Plate I; Plate III, Fig. 7; Plate IV, Fig. 7a). At no point in this region, however,

is there the least indication of fusion or connection with this root. Just below this root the ganglion is in contact with a portion of the lateral border of the cutaneous ganglion. This anterior portion of the ventral lateralis ganglion comprises, in most specimens, the greater portion of its bulk. Just posterior to the point of origin of the second branchial trunk, the ganglion becomes perceptibly smaller, sometimes dwindling away to a mere layer only a cell or two in thickness, closely applied to the surface of the visceral ganglion. Occasionally beyond this point it seems to disappear completely for a few sections. This suggests the idea that it may consist primitively of two ganglia, one anterior, the other posterior. To settle this point further study is necessary.

It may be noted here that all of the lateralis ganglia, in VII, IX, and X, invariably lie lateral to any other ganglia that may happen to be in the same horizontal plane with them. A glance at the reconstruction (Plate I) will make this evident. The same thing is true of the lateralis ganglia in the embryo of *Rana*, as shown by the reconstructions accompanying the paper of Landacre and McLellan.

No separate root of the ventral lateralis X ganglion could be found in any of the stages studied. Although, as stated above, the ganglion comes into close proximity to the dorsal lateralis root, no fibers pass from it to this root in this region. It is noteworthy that in the embryo of *Rana*, likewise, no separate root of the ventral lateralis X ganglion was found.

From the posterior end of the ventral lateralis X ganglion arises the lateralis component of the visceral trunk, the *ramus lateralis inferior* (Plate I, *R. L. i. X*), which passes ventro-caudad in company with the remaining components of the visceral trunk. In most transverse sections it is extremely difficult to be certain of the presence of this component in even the most proximal portion of the trunk. In parasagittal sections, however, the relation of its fibers to the cells of the ventral lateralis ganglion is absolutely unmistakable.

In the region of the origin of the branchial trunks from the visceral ganglion, the ventral lateralis ganglion presents very strongly an appearance of contributing fibers to these trunks, and this appearance is given added force by the large size of the ganglion in this region, coupled with the fact that no other ramus arises from this portion. It is true that the rela-

tions here are confused by the fact that fibers of another component, either cutaneous or motor (possibly both), passing down from the cutaneous ganglion, and then between the ventral lateralis and visceral ganglia, enter the branchial trunks at this point. Nevertheless, the appearance mentioned is too striking and too definite to be explained entirely as due to confusion with these other fibers.

But, in spite of repeated and most careful study of this point, I have not succeeded in tracing fibers from the branchial trunks to unmistakable lateral line organs. Moreover, Coghill found no lateralis fibers in these trunks in the late larval stage of *Ambystoma*, and, to the best of my knowledge, they have not been described as present there in any other form, either among fishes or Amphibia.

What, then, is the significance of this rather large mass of cells making up the anterior and larger portion of what I have called the ventral lateralis ganglion? One possibility that naturally occurs to one is that this ganglion actually sends lateralis fibers into the branchial trunks in the embryo, but that this is merely a rudimentary and transitory condition, disappearing by the time the late larval stage is reached. I am forced to say that, considering all the relevant facts, this hypothesis does not seem a very probable one. Another, and even more extreme possibility, is that this group of cells is not part of the lateralis system at all; that it is, perhaps, a special visceral ganglion, which sends gustatory fibers down the branchial trunks to innervate taste-buds in the region of the gills. It will be recalled that the cells comprising the most ventral portion of the ventral lateralis IX ganglion similarly give the appearance of sending fibers into the glossopharyngeal trunk, where I have not been able to demonstrate the presence of lateralis fibers by following the distribution, and where, likewise, they have never been found in other vertebrates.

Strong evidence against the possible special visceral character of these portions of the ventral lateralis IX and ventral lateralis X ganglia is afforded by their histological character. (See p. 252). The lateralis ganglia in general present the most distinctive appearance of any of the components, largely due to the uniformly larger size, rounded form, and lighter staining reaction of their cell nuclei. In these and all other respects that I have noted, the questionable portions of the two ganglia under

discussion are absolutely indistinguishable from any other portions of any of the lateralis ganglia. In the few cases where special visceral ganglia have been definitely identified in embryonic stages, as in *Ameiurus* (Landacre, 1910) and in *Lepidosteus* (Landacre, 1912), their histological appearance has been unmistakably different from that of the lateralis ganglia.

It is interesting to note that a number of rather small lateral line organs are present on the operculum, close to the bases of the gills; but, while fibers from the branchial trunks can be readily followed to this general region, and pass in close proximity to these lateral line organs, I have not been able to trace them to the organs with certainty.

Motor X component. The motor component of X leaves the medulla by several areas of exit. A portion of the fibers leave the medulla just ventral to the area of entry of the large cutaneous and visceral root; the rest by three other areas of exit, at about the same level, and posterior to this point. The fibers from these posterior areas of exit pass forward to the visceral and cutaneous root, and are soon indistinguishable among its fibers. Their further distribution was not studied.

HISTOLOGICAL CHARACTERS OF THE GANGLIA.

The nuclei of the cells of the cranial ganglia, in the preparations studied, stand out for the most part with great distinctness. The chromatin is not collected largely in a central nucleolus, as is the case in the embryo of *Rana*, but is distributed rather uniformly throughout the nucleus. (Compare detail drawings, Plate IV, with similar drawings accompanying Landacre and McLellan's paper on *Rana*.) The limits of the cytoplasm of the individual cells it is usually impossible to make out, at least within the ganglia. It is apparent, therefore, that any histological differentiation between the different ganglia that we may be able to recognize must be largely a matter of the appearance of the nuclei of the cells.

The size, shape, and depth of staining of the nuclei in a given ganglion, or in the ganglia belonging to a given system (cutaneous, lateralis, etc.) varies considerably. Nevertheless, this variation in a given case has its limits, as far as any considerable number of the nuclei are concerned, and, with the exception of cases which will be discussed below, the ganglia of a given system have a fairly uniform appearance.

In the 11.5 mm. embryo the most striking contrast in histological appearance between different ganglia is that between the lateralis ganglia and all the others. The nuclei of the cells of the lateralis ganglia are larger and rounder, and do not stain as heavily with Delafield's hæmatoxylin as do the nuclei of other ganglia. (See Plate IV, Figs. 1a, 2a, 3a, 5a, 6a, 7a, 8a, and 9a). They thus stand out in strong contrast, and even when the lateralis ganglia are practically fused with other ganglia, the limits of each are readily recognized by reason of these differences.

In stages younger than the 11.5 mm. embryo, these differences become less pronounced, and in the earliest stage where the ganglia are distinctly recognizable, can hardly be detected. The degree of contrast varies also in different specimens to a very great extent, due probably, largely if not entirely, to differences in fixation, staining, etc.

Between the cutaneous and visceral ganglia it is harder to detect differences of histological appearance. On the whole, the nuclei of the visceral ganglia seem to stain a little heavier than those of the cutaneous ganglia, for the most part are packed together a little closer, and perhaps average a trifle smaller. The variation is considerable, however, and sections can be found showing exactly the reverse condition.

Of the two regions of the auditory ganglion spoken of on page 239, the nuclei in the more anterior and dorsal region are very slightly larger, slightly lighter-staining, and not packed quite so close together as those in the ventro-posterior portion. These differences are exceedingly slight in the 11.5 mm. embryo; in the oldest of the early larval stages studied they have become much more pronounced, and the contrast between the two regions of the ganglion is very striking.

In the earlier embryonic stages studied two kinds of coloring material are present in the cytoplasm of the ganglion cells: yolk granules and pigment granules. The latter, as seen under the 4 mm. objective, are mere specks, of a brownish color, and identical in appearance with the pigment granules visible at the same time in the cells of the ectoderm. The yolk granules are larger, of various shapes, and stain much like the cytoplasm itself—usually a little darker. As development proceeds these yolk granules are apparently absorbed; in the 11.5 mm. embryo they are no longer present in the ganglion cells, though still

numerous in muscle and loose mesenchyme cells. At the same time the pigment granules undergo changes. In the 11.5 mm. embryo the lateralis ganglia are for the most part well pigmented, but the pigment, now of a yellowish-brown color, is uniformly spread through the cytoplasm of the cells, and the individual granules are not visible under the 4 mm. objective. In the other ganglia, the pigment is almost entirely absent. This furnishes another means by which, in many preparations, the lateralis ganglia are readily distinguished from the others.

SUMMARY.

In late larval and adult stages of urodeles the ganglia of the cranial nerves are usually closely fused into three ganglionic masses. To learn the primary relations of the individual ganglia of these nerves, embryonic stages must be studied in which this fusion has not yet taken place, or in which it has not proceeded very far. The descriptions in this paper are of such stages.

In the 11.5 mm. embryo of *Ambystoma jeffersonianum*, the more general relations of the ganglia of the V and VII nerves are essentially the same as reported by Coghill in the late larval stage of *Ambystoma tigrinum*.

The Gasserian or cutaneous V ganglion lies close to the lower portion of the anterior end of the medulla, in the region between the optic and auditory vesicles. At this stage a separate profundus portion can not be distinguished in the Gasserian, but this distinction is very marked in the earlier stages.

The dorsal lateralis VII ganglion lies dorsal to the Gasserian ganglion.

The geniculate or visceral VII ganglion is posterior to the Gasserian, and except for its most ventral portion, lies in the space between the auditory vesicle and the medulla.

The ventral lateralis VII ganglion lies under the anterior end of the auditory vesicle, ventro-laterad of the geniculate ganglion, to which its proximal end is fused.

Only a single auditory ganglion could be recognized, in which, however, two different regions could be distinguished. These are characterized by histological differences, which are much more marked in the later stages studied.

In essential features the IX-X complex in the 11.5 mm. embryo is similar to that reported by Landacre and McLellan in *Rana*.

The visceral IX ganglion (*G. petrosum*) is quite separate from the visceral X; it lies just posterior to the auditory vesicle.

In earlier stages two distinct lateralis ganglia are present on IX, one of which gives rise to the ramus supratemporalis, the other to the lateralis component of the ramus auricularis. In the 11.5 mm. embryo these have united; the combined ganglia lie dorsal to the visceral IX.

Of the ganglia of X, the cutaneous or jugular is most mesial, and is close to the medulla. The cutaneous component of the ramus auricularis was the only component from it that was recognized with certainty, but its large size makes it probable that it sends components to other nerves as well.

The visceral X ganglion (*G. nodosum*) has a position posterior to the visceral IX and lateral to the cutaneous X. In stages earlier than the 11.5 mm. embryo it is divided by a constriction in its middle part into two portions, the more anterior giving rise to the two branchial trunks, the more posterior to the visceral trunk.

As in all the other urodeles hitherto studied, all the root fibers from the lateralis ganglia of IX and X unite into one large common root before entering the medulla. The area of entry of this root is the most anterior of all the roots of IX and X, being slightly farther cephalad than the visceral root of IX.

The dorsal lateralis X ganglion lies dorsal to the visceral X ganglion.

The ventral lateralis X ganglion lies throughout its extent in close contact with the dorso-lateral surface of the visceral X ganglion. In the 11.5 mm. stage it is partially fused with the ventral border of the dorsal lateralis X ganglion; later it becomes fused with dorsal lateralis IX also. No separate root of this ganglion could be identified.

The greater bulk of the ventral lateralis X ganglion is in the region of the branchial trunks, and it has here the appearance of contributing fibers to these trunks. Whether this is actually the case could not be definitely settled; our knowledge of the character of the branchial trunks in late larval stages

of Ambystoma and other forms would not lead us to expect to find lateralis fibers in them in the embryo. The character of this anterior portion of the ganglion is not considered definitely settled.

Except in the earliest embryonic stages, the nuclei of the cells of the lateralis ganglia are uniformly larger, rounder, and lighter-staining (with Delafield's hæmatoxylin) than those in the other ganglia. The differences between the nuclei of cutaneous and visceral ganglia are slight and not constant.

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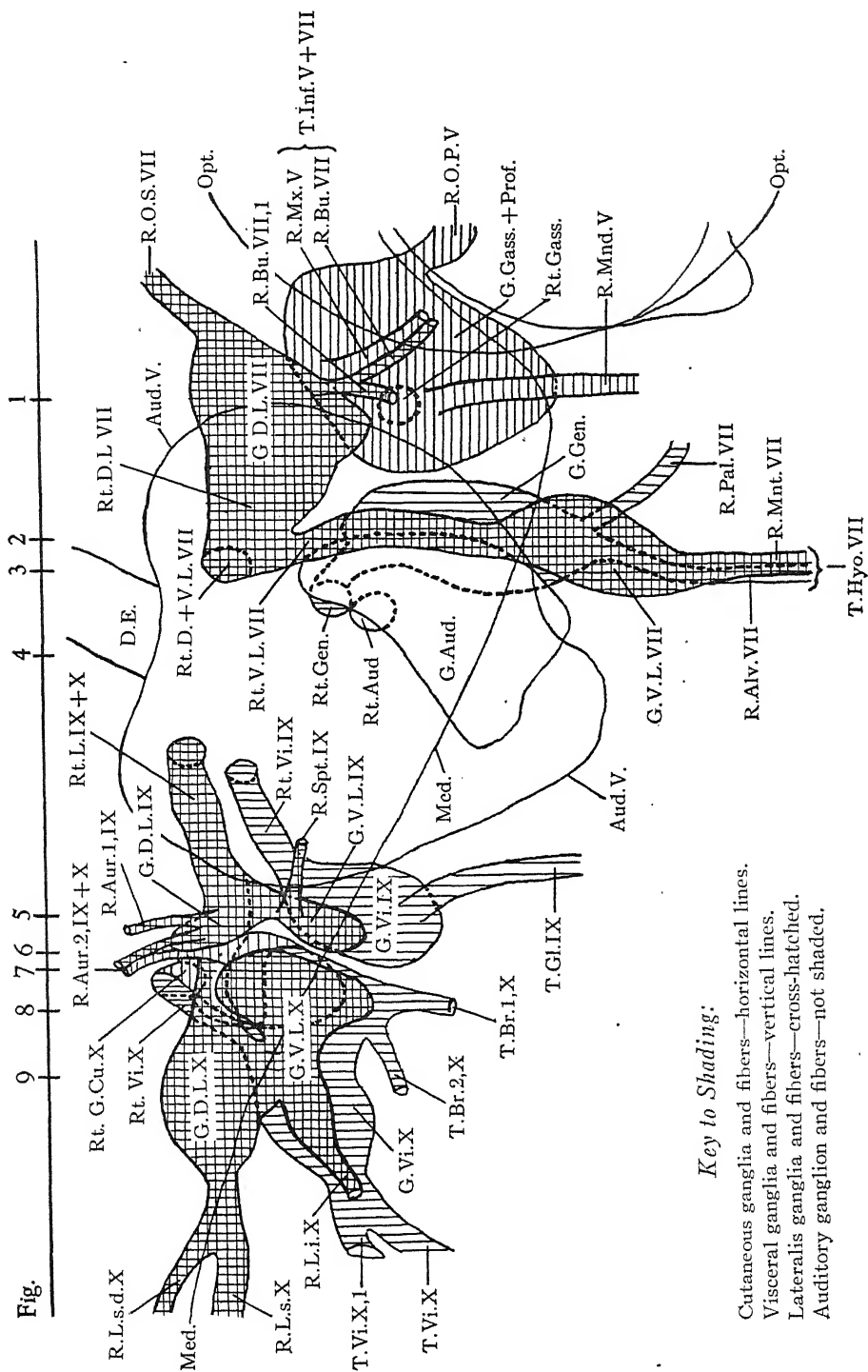
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PLATE I.

A reconstruction of the cranial ganglia of an 11.5 mm. embryo of *Ambystoma jeffersonianum*, being a projection of these ganglia (from the right side of the head) upon the median, vertical plane of the head. The roots of the ganglia and the proximal portions of the chief nerves are shown, but motor components are omitted. The auditory vesicle, part of the optic vesicle, and the base of the brain are shown in outline. The areas of entry of the sensory roots into the medulla are indicated. Above the reconstruction are shown the positions of the sections figured in the following plates. Magnification, $\times 150$.

ABBREVIATIONS.

- Aud. V.*—outline of auditory vesicle.
B. V.—blood vessel.
D. E.—ductus endolymphaticus.
En.—outgrowth of endoderm from lateral angle of pharynx.
G. Aud.—auditory ganglion.
G. Cu. X—cutaneous X ganglion.
G. D. L. VII—dorsal lateralis VII ganglion.
G. D. L. IX—dorsal lateralis IX ganglion.
G. D. L. X—dorsal lateralis X ganglion.
G. Gass. (+Prof.)—Gasserian ganglion, into which profundus ganglion has been incorporated.
G. Gen.—geniculate ganglion.
G. Vi. IX—visceral IX ganglion.
G. Vi. X—visceral X ganglion.
G. V. L. VII—ventral lateralis VII ganglion.
G. V. L. IX—ventral lateralis IX ganglion.
G. V. L. X—ventral lateralis X ganglion.
H. C.—horizontal canal of auditory vesicle.
M.—muscle.
M. d. m.—depressor mandibulæ muscle.
Med.—medulla; in reconstruction, base of medulla.
M. l. d.—longissimus dorsi muscle.
M. l. d. i.—longissimus dorsi inferior muscle.
M. ma.—masseter muscle.
Mo. VII—motor component of VII.
M. tem.—temporalis muscle.
No.—notochord.
Opt.—outline of optic vesicle.
Pal. B.—palatoquadrate bar.
Par.—parachordal.
Phar.—pharynx.
R. Alv. VII—ramus alveolaris VII.
R. Aur. 1, IX—ramus auricularis 1, IX.
R. Aur. 2, IX + X—ramus auricularis 2, IX + X.
R. Aur. ?—branch of auricularis?
R. Bu. VII—ramus buccalis VII.
R. Bu. VII, 1—first branch of ramus buccalis VII.
R. L. i. X—ramus lateralis inferior X.
R. L. s. X—ramus lateralis superior X.
R. L. s. d. X—dorsal branch of ramus lateralis superior X.
R. Mnd. V—ramus mandibularis V.
R. Mnt. VII—ramus mentalis VII.
R. Mnt. VII, 1—first branch of ramus mentalis VII.
R. Mx. V—ramus maxillaris V.
R. O. S. VII—ramus ophthalmicus superficialis VII.
R. O. P. V—ramus ophthalmicus profundus V.
R. Pal. VII—ramus palatinus VII.
R. Sac. VIII—ramus acusticus sacculi.
R. Spt. IX—ramus supratemporalis IX.
R. Utr. VIII—ramus acusticus utriculi.
Rt. Aud.—root of auditory ganglion.
Rt. Cu. X—root of cutaneous X ganglion.
Rt. D. L. VII—root of dorsal lateralis VII ganglion.
Rt. D. + V. L. VII—root of dorsal and ventral lateralis ganglia of VII.
Rt. Gass.—root of Gasserian ganglion.
Rt. G. Cu. X—cutaneous X root and ganglion.
Rt. Gen.—root of geniculate ganglion.
Rt. L. IX + X—lateralis root of IX and X.
Rt. L. X—lateralis root of X.
Rt. Mo. X—motor root of X.
Rt. Vi. IX—root of visceral IX ganglion.
Rt. Vi. X—root of visceral X ganglion.
Rt. V. L. VII—root of ventral lateralis VII ganglion.
T. Br. 1, X—truncus branchialis 1, X.
T. Br. 2, X—truncus branchialis 2, X.
T. Gl. IX—truncus glossopharyngeus IX.
T. Hyo. VII—truncus hyomandibularis VII.
T. Inf. V + VII—truncus infra-orbitalis V + VII.
T. Vi. X—truncus visceralis X.
T. Vi. X, 1—first branch of truncus visceralis X.



Key to Shading:

Cutaneous ganglia and fibers—horizontal lines.

Visceral ganglia and fibers—vertical lines.

Lateralis ganglia and fibers—cross-hatched.

Auditory ganglion and fibers—not shaded.

PLATE II.

(Shading as in Plate I; in addition, motor components in solid black.)

Fig. 1. A camera outline drawing of a portion of a section through the head of an 11.5 mm. embryo of *Ambystoma jeffersonianum*. The section passes through the dorsal lateralis VII ganglion (*G. D. L. VII*) and the Gasserian ganglion (*G. Gass.*). The position of this section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 1a.

Fig. 2. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the geniculate (*G. Gen.*) and ventral lateralis VII (*G. V. L. VII*) ganglia. The junction of the roots of the dorsal and ventral lateralis VII ganglia is shown. The position of this section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 2a.

Fig. 3. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the geniculate (*G. Gen.*), auditory (*G. Aud.*), and ventral lateralis VII (*G. V. L. VII*) ganglia. The position of this section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 3a.

Fig. 4. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the posterior part of the auditory ganglion (*G. Aud.*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 4a.

Fig. 1.

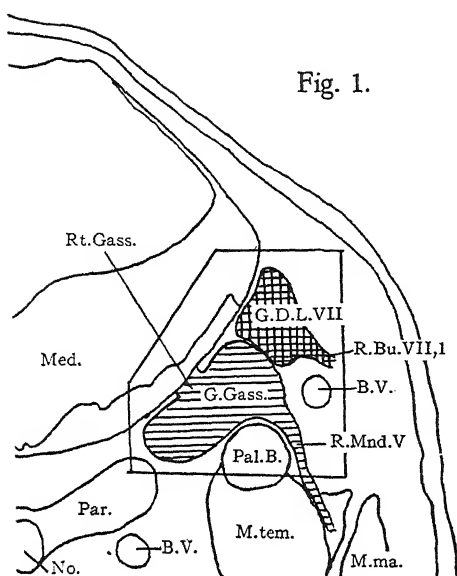


Fig. 2.

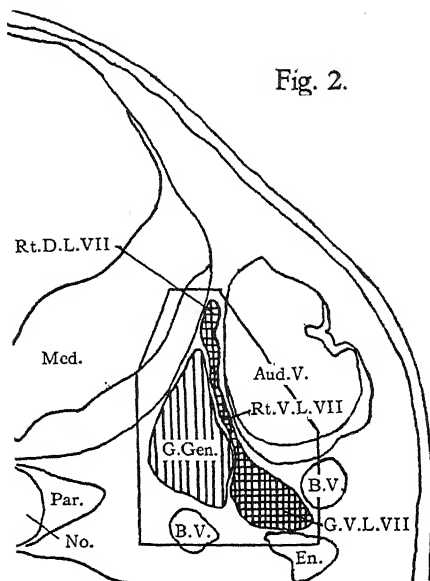


Fig. 3.

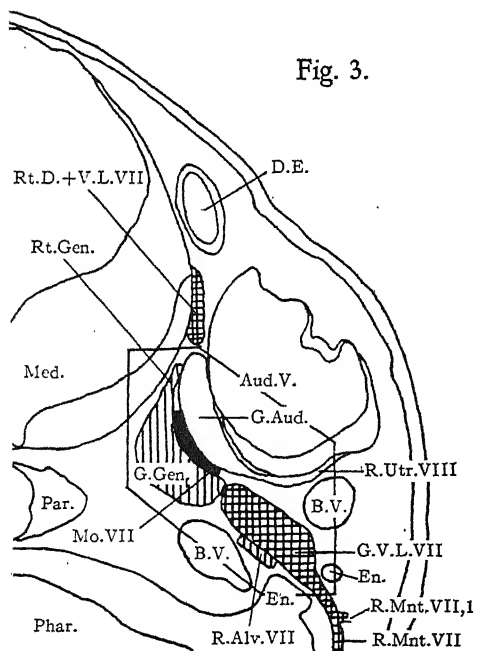


Fig. 4.

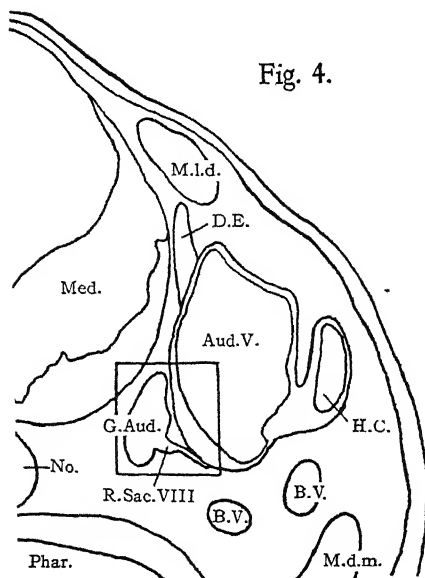


PLATE III.

(Shading as in Plate I; in addition, motor components in solid black.)

Fig. 5. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo of *Ambystoma jeffersonianum*. The section passes through the ventral lateralis IX ganglion (*G. V. L. IX*) and the visceral IX ganglion (*G. Vi. IX*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 5a.

Fig. 6. A camera outline drawing of a portion of a section through the head of an embryo of *Ambystoma jeffersonianum*, slightly older than the 11.5 mm. stage from which all the remaining drawings and the reconstruction were made. The section passes through both dorsal and ventral lateralis IX ganglia (*G. D. L. IX*; *G. V. L. IX*); through the visceral IX ganglion (*G. Vi. IX*); the cutaneous X ganglion (*G. Cu. X*); and through the root of the dorsal lateralis X ganglion (*Rt. L. X*). The position of the corresponding section of the 11.5 mm. embryo in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 6a. (The relationship of lateralis and cutaneous components of the ramus auricularis could not be well shown in any one section of the 11.5 mm. embryo from which all the remaining drawings were made.)

Fig. 7. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo of *Ambystoma jeffersonianum* used in making all drawings except Figs. 6 and 6a. The section passes through the cutaneous X ganglion (*G. Cu. X*); the root of the dorsal lateralis X ganglion (*Rt. L. X*); the ventral lateralis X ganglion (*G. V. L. X*); the visceral X ganglion (*G. Vi. X*); and the visceral IX ganglion (*G. Vi. IX*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 7a.

Fig. 8. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the cutaneous X ganglion (*G. Cu. X*); the ventral lateralis X ganglion (*G. V. L. X*); and the visceral X ganglion (*G. Vi. X*); also through the anterior tip of the dorsal lateralis X ganglion (*G. D. L. X*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 8a.

Fig. 9. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the visceral X ganglion (*G. Vi. X*) and the fused dorsal and ventral lateralis X ganglia (*G. D. L. X* and *G. V. L. X*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, $\times 80$. The details of the area blocked out are shown in Plate IV, Fig. 9a.

Fig. 5.

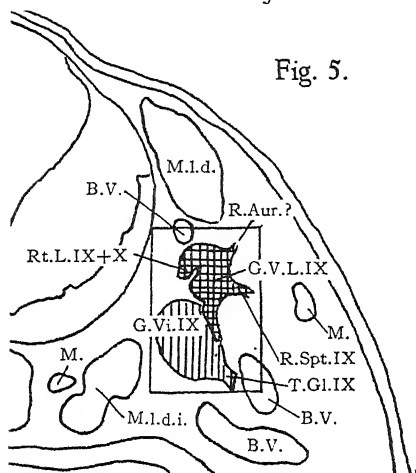


Fig. 6.

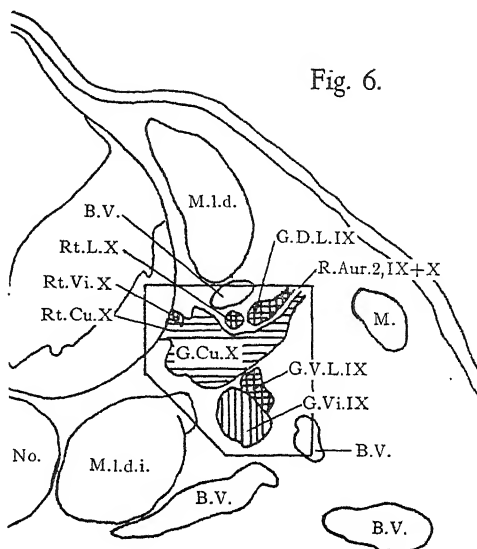


Fig. 7.

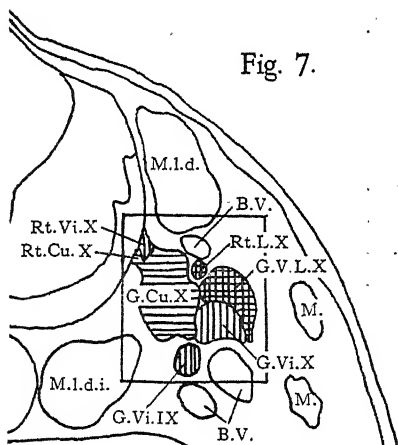


Fig. 8.

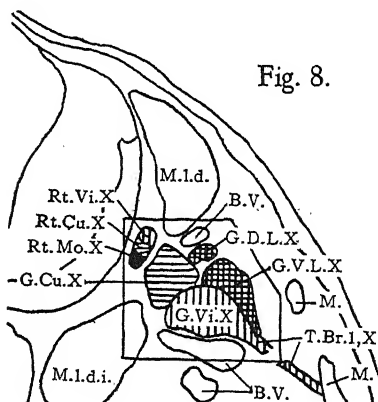


Fig. 9.

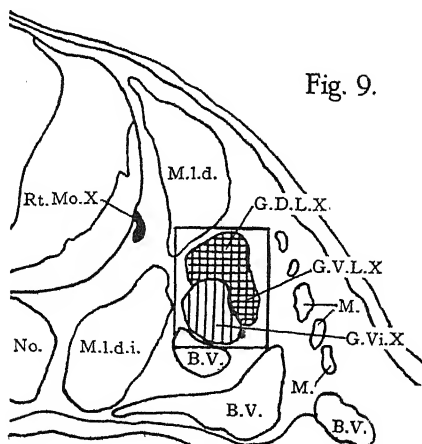


PLATE IV.

- Fig. 1a. Details of area blocked out in Fig. 1. Magnification, $\times 132$.
Fig. 2a. Details of area blocked out in Fig. 2. Magnification, $\times 132$.
Fig. 3a. Details of area blocked out in Fig. 3. Magnification, $\times 132$.
Fig. 4a. Details of area blocked out in Fig. 4. Magnification, $\times 132$.
Fig. 5a. Details of area blocked out in Fig. 5. Magnification, $\times 132$.
Fig. 6a. Details of area blocked out in Fig. 6. Magnification, $\times 132$.
Fig. 7a. Details of area blocked out in Fig. 7. Magnification, $\times 132$.
Fig. 8a. Details of area blocked out in Fig. 8. Magnification, $\times 132$.
Fig. 9a. Details of area blocked out in Fig. 9. Magnification, $\times 132$.

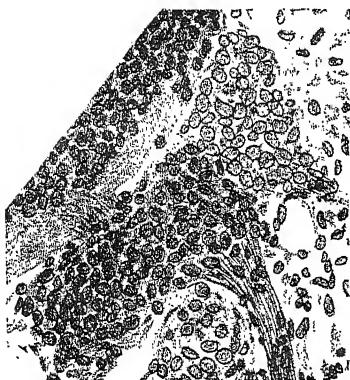


Fig. 1a.

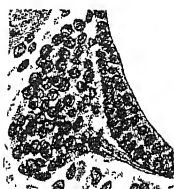


Fig. 4a.

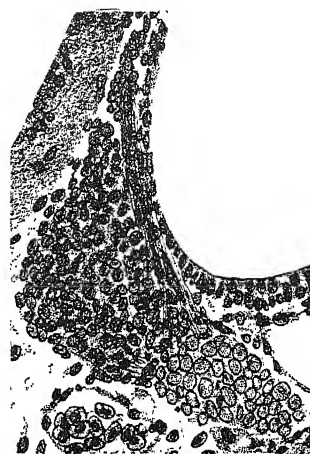


Fig. 2a.



Fig. 3a.



Fig. 5a.

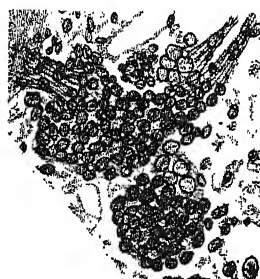


Fig. 6a.



Fig. 7a.

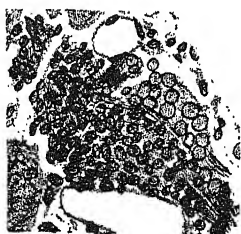


Fig. 8a.



Fig. 9a.

THE OHIO JOURNAL OF SCIENCE

VOL. XXIV

NOVEMBER, 1924

No. 6

THE INTESTINE OF THE MINNOW CAMPOSTOMA ANOMALUM (RAFINESQUE), WITH SPECIAL REFERENCE TO THE DEVELOPMENT OF ITS COILING.*

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I. INTRODUCTION.

Fishes of the genus *Campostoma* (Cyprinidæ) are characterized by an intestine which is coiled around the air bladder, a structural peculiarity found in no other known fishes. At the suggestion of Professor R. C. Osburn the writer undertook a study of the development, in post-embryonic life, of this intestinal coiling in *Campostoma anomalum* (Rafinesque), and the anatomy of such parts of the canal as would be essentially involved in this general problem.

During the summers of 1920 and 1921, when the writer was a member of a state fish survey party under Dr. Osburn, for the

*Dissertation presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School of the Ohio State University.

Contribution number 76, from the Department of Zoology and Entomology, Ohio State University.

Ohio Division of Fish and Game, very many of this species were taken with the seine in various Ohio waters. Some were contributed by a small field party of 1922, and during the same spring and summer the writer collected numerous, mostly young specimens in creeks in the vicinity of Columbus. A total of 600 specimens were studied.

The writer wishes to express his indebtedness to Prof. R. C. Osburn, Head of the Department of Zoology and Entomology, Ohio State University, who gave valuable aid and suggestions; to Mr. Carl L. Hubbs, Curator of fishes, Museum of Zoology, University of Michigan, for help in determination of immature specimens, to a number of Ohio State colleagues who helped with the seine, and to his wife for the averaging of hundreds of fish measurements to get final data in table 2.

II. ANATOMY OF THE INTESTINE.

(A) *General Structure.*

The intestine in *Campostoma* adults appears to be a closely wound spiral, which surrounds other parts of the digestive system and the air bladder, (Plate VI, Fig. 67). However, a small anterior portion of the air bladder is not dorsally covered in any specimens, though it had previously been described (Jordan and Evermann, 1896, p. 204) as "entirely surrounded by many convolutions of the long alimentary canal."

The intestine length is not remarkable for other Cyprinidæ which are essentially vegetable feeders or limnophagous, have a long intestine. In *Pimephales promelas* it is as long as in *Campostoma*. Coiling necessarily occurs in various groups of vertebrates, wherever a lengthy intestine exists; but only in this one genus is there a transverse coiling, passing intestinal loops dorsally over air bladder.

Gonads are not enclosed within intestinal coils, (Plate VII, Fig. 100), though they have been described as thus enclosed, (Jordan and Evermann, 1896, p. 294). The relation of gonads to canal is discussed in a later part of this paper.

In a small percentage of cases all dorsal intestinal loops are lacking, the air bladder being completely exposed dorsally. These thus show no conformity to the intestinal arrangement used as the first diagnostic character in classification keys.

The oesophagus in *Campostoma*, as in other fishes, is a short tube, scarcely projecting posteriorly into the coelom. Anteriorly it widens into pharynx. Posteriorly it widens out into the thickest part of the canal, from which to be sure it is not separated by any constriction. The oesophagus itself was not studied.

The thickest part of the alimentary canal, the apparent stomach, (the nature of which will be discussed below) has a diminution in diameter posteriorly. The canal passes with a very pronounced, sharp bend, at the posterior end of the abdominal cavity, into the long intestine, but with no pyloric valve or any other constriction. The intestine is small and of practically uniform diameter throughout, except near the anus, where it tapers down somewhat more. There is no large intestine.

In the very young *Campostoma* the canal is short and simple, consisting (between oesophagus and anus) of three straight portions bent upon each other like parts of a flattened letter Z. The comparison to a letter Z is distinctly better in this case than the letter S, sometimes used in such alimentary canal descriptions. At first all of the first or anterior of the three canal parts, the thickest of the three, was thought of as stomach. The adult intestinal condition is the result of an extensive coiling process during growth, principally of the middle and end parts of the Z-shaped canal.

(B) *Detailed Study of the Intestine With Special Reference to Absence of Stomach and Nature of Mucosa Surface.*

Of the original three-part alimentary canal seen in coelom in youngest free-swimming fish, it was first thought (as already suggested), that all of the first, or anterior enlarged part was stomach, and the other parts intestine, but examination demonstrated such demarcation impossible, and raised new questions.

The same interesting problem has been considered in many other Cyprinidæ, all European. The condition described below for *Campostoma* will be clarified by noting first the prevalence of similar conditions in other minnows, as indicated in the literature.*

*Papers which are probably the most important on both histological and physiological treatment of alimentary canal of minnows are listed in the bibliography.

Yung (1899) summarized and discussed previous work, from which it appears that Bischoff (1838) concluded a stomach properly speaking was lacking in a number of Cyprinidæ. Valatour (1861), Luchau (1876), Edinger (1877), and others contributed materially to the evidence. 'Oppel (1896-97) summarized all existing information comprehensively. Pictet (1909) added careful histological work on several species, and reviewing literature, made adequate generalization of the very uniformly accepted conclusions. Part of his summary is quoted here in translation. (Pictet, 1909, pp. 52, 55, 56).

"The intestine properly so-called of the Cyprinoid fishes directly follows the oesophagus, and there is no stomach in the histological sense of the word."

"* * * their intestine * * * continues to the anus without morphological differentiation other than the enlargement of the anterior part."

"The principal reasons which have been given in favor of this view are the following: (1) Complete absence of gastric glands in the swollen part of the digestive tube. It is known that in fishes pepsin glands exist only in the stomach. (2) The fact that the hepatic duct opens, in the stomach-less fishes, 2 or 3 mm. from the oesophagus, while in general it is back of the stomach and opens into the anterior part of the mid-intestine."

"To these arguments which in themselves suffice to show that the swollen part of the intestinal tract should be considered not as stomach, but as anterior portion of the intestine, we can add the following: (3) The mucosa of the stomach of fishes is generally covered with fine folds, while the intestine possesses high, irregular folds; a well defined limit (pyloris) exists between the two parts. But in these fishes large folds appear at the oesophagus and are found to be identical up to the anus, without any demarcation between the swollen part and the rest of the digestive tube."

"(4) There are never any goblet cells in the epithelium of the stomach. In the fishes with which we are concerned, the histology shows us that they occur from the oesophagus to the anus."

"(5) Physiology conforms this view; the reactions of the part in question are in Cyprinidæ alkaline or neutral, as in the intestine of fishes in general, while the reactions of the stomach are most often acid."

“(6) Finally there is no difference between the inner structure of the epithelial cells of the swollen part of the intestine, and that of the cells of the rest of the tube, while in most fishes with differentiated stomach, the cells of the two regions have a different aspect.”

In *Campostoma*, after some development of the alimentary canal, the anterior section of the canal in the coelom, the apparent stomach, becomes differentiated into a more swollen anterior half, having somewhat thicker walls, and a posterior half, remaining less thick. The latter to a small extent does take part in some subsequent coiling, but the anterior does not.

The gall bladder, somewhat difficult to see unless probed for, is joined to the canal by a common bile duct near the mid-point of the entire anterior section, (Plate IV, Fig. 46). Obviously then the thinner posterior half of this long anterior section cannot be stomach.

Still the anterior swollen part, anterior to bile duct, might be stomach, and in older specimens it does look somewhat different than the smaller posterior part. If stomach there would have to be a pyloric valve to separate effectively the acid digestive chamber from the alkaline. There is no indication whatever of pylorus in front of bile duct junction, in any specimens examined. Even if reactions were different the mixing might be but slight because of steady passage of the large mass of canal contents, to prevent appreciable flow anteriorly.

The common bile duct entrance, however, is not quite so far forward as in some other minnows. Of several European species, Edinger (1877) says: “The common bile duct opens at the end of the oesophagus.” Valatour (1861) says: “Nearly at the beginning of this swollen part the choleduchal canal opens out.” Yung (1899) says: “The choledochal canal enters the intestine immediately behind the oesophagus.” In a large *Campostoma* of about 80 mm. length, in which the entire originally anterior canal section was 35 mm. long, nearly 29 mm. preceded the common bile duct junction. This, and other measurements essentially no different, suggest room for a histologically differentiated stomach.

Investigation was briefly made into the nature of the chemical condition in alimentary canal. Parts from freshly stunned specimens were opened. Intestinal contents and

scrapings from wall were all used and mashed to free possible digestive juices. In some small specimens where that was impracticable, small parts of the canal were completely mashed and used. In the rather dense intestinal contents no secretions were recognized. Whether specimens in best condition for this purpose were selected could not be determined.

To make the tests a small quantity of mashed substance was placed in white porcelain dish, neutral water added, and drops of the indicator added to the liquid. To what extent the color reactions were of digestive secretions only, rather than also materially of plant substances, etc., is impossible to say. Some better technique must be developed for H ion determination of this particular type.

Since tests gave practically uniform results on material from half a dozen specimens, these may be given here as pertinent at least for conditions worked under. Merely general conclusions seem necessary here. Material for a short distance back of common bile duct junction, showed invariably a weak alkaline reaction. Material from in front of this junction, that is, from the anterior swollen part, showed invariably a very slight acid reaction. It was never quite neutral or alkaline. This acidity, a true stomach property, was unexpected here, in view of the preceding structural evidence of the lack of a true stomach.

The folds of the inner surface of the intestine are conspicuous, especially in the swollen part of the canal. They are on a zig-zag plan, and in superficial view seem quite regular. Oesophagus folds were not examined.

The zig-zag formation has been found in other Cyprinidæ. In these and a few other fishes, there is, according to Edinger (1877), rather than the plan of fully developed crypts of many other Teleosts, "a tendency to the primitive system existing in Cyclostomes, and most Selachii, of simple, lengthwise folds without crypts. Thus the mucosa ridges of *Pleuronectes solea* are arranged one near another without cross connection. They pass in zig-zag direction through the entire intestine."

Pictet (1909, pp. 58, 59), found zig-zag folds in *Cyprinus carpio*, *Carassius auratus*, *Tinca vulgaris*, *Leuciscus rutilus*, and *Barbus fluviatilis*, but there were differences in detail according to species, and in one at least according to age; but he found no differences between the swollen part and the thinner intestine following.

The *Campostoma* mucosa surface zig-zags are similarly unbroken ridges, (Plate VII, Figs. 94, 95). They are not as irregular as in the so-called herring bone weave pattern pictured by Breder and Crawford (1922, Figs. 124-126), for *Leuciscus* and *Notropis*. Only occasionally there occurs a break, or anastomosis, or a slight branch. The V-shaped units of neighboring zig-zags in column, more distinctly impress the eye than the long continuous zig-zag ridges separately. The direction of the sides of the Vs is nearly in the circular direction of the canal, or much more transverse than longitudinal. This suggests transverse folds, but a little study shows this to be due wholly to appearance produced by these acute-angled Vs so directed. In other words the ridges and grooves are longitudinal, but pass in very indirect, zig-zag paths.

For detailed study of intestinal mucosa pieces about 3 mm. long were cut from selected places and the circular surface spread out flat. A large portion of such area was drawn with camera lucida.

The wall of the alimentary canal was found rather thin and translucent, except in a few specimens, where it was considerably thicker and opaque, and in which also the folds were more prominent, so that a cross section through intestine in such thick wall in widest canal part, showed grooves to be almost half as deep as the diameter of the free lumen of the canal. But in all typical cases, which included a great majority of all available specimens, the grooves were relatively much shallower. These typical ones are exclusively referred to in this study.

The typical arrangement is seen, (Plate VII, Fig. 95) in the swollen part, anterior to bile duct junction. For a short distance at the very anterior end of this swollen part, the grooves are even a little deeper, (Fig. 94). Any apparent irregularities in this are due entirely to the fact that the ridges being higher are subject to tilting, with formation often of wavy upper edges. The condition exactly as in Fig. 95 is found not only in most of the swollen part, but also for a little distance in back of bile duct junction. A little farther back the ridges become lower and lower, and also narrower. The Vs are smaller. The grooves then are much smaller, but relatively wider.

After considerable decrease in size of Vs, some variable distance posteriorly there is a modification in that the Vs become isolated by dropping out of parts of ridges, (Plate VII, Fig. 96).

Half of the intestine may be like this. Following comes a longer or shorter portion in which the original Vs are broken up so much that merely short bars (portions of the former sides of the Vs) remain. Often quite a number of these in a specimen, instead of being straight, take the form of small wide-angled Vs in the opposite direction from the original larger Vs (Fig. 97). Still farther posteriorly the bars are shortened still more and lie in a general transverse direction. Where this modification exists there is the appearance of transverse folds, but the explanation shows how this peculiar condition is obtained. Finally in all specimens examined, ridges fade out entirely at some short but variable distance in front of the anus, so that at the end the intestine is entirely without mucosa folds.

The similarity of folds directly anterior and posterior to the bile duct junction, instead of the presence of a different set of fine stomach folds (point 3 in Pictet's summary on conditions in Cyprinidæ), shows the lack of a specialized stomach mucosa in *Campostoma*.

No attempt was made to work out the development of the folding of intestinal mucosa during growth of the fish. Adult specimens only were considered in this work.

Further investigation into question of lack of true stomach was made by microscopical examination of epithelium. Considerable difficulty was experienced in getting satisfactory sections. Specimens were practically always rather filled with food and inorganic material, (Kraatz, 1923, p. 276), which are an obstruction to sectioning. From a few specimens successfully cleaned without injuring mucosa, the following parts were sectioned: portion of swollen region, at region of bile duct junction, posterior to that junction, at about the middle of the long intestine, and also nearer the end. Bouin's and Zenker's fixatives were tried, and sections stained with Delafield's haematoxylin and eosin.

Merely a short general treatment of the histological examination of epithelium will be given. There is a regular columnar epithelial layer, one cell layer thick. Cells are practically alike in size and form on all ridges and in grooves, in different parts of intestine, and in different specimens also, despite any differences in size of folds. Moreover, the cells are the same in the swollen part as behind the bile duct entrance, instead of being of a specialized type, as they would in a true stomach, (point 6 in

Pictet's summary). Such epithelium is described by Pictet (1909, p. 57), and more fully by Oppel, (1896, pp. 35, 72).

Goblet cells are present in the columnar epithelium, but do not seem abundant. They are also present in the swollen part, though possibly less numerous there. Since goblet cells are never found in a true stomach, (point 4 in Pictet's summary) this swollen part in *Campostoma* cannot be differentiated from intestine parts following, and therefore cannot be identified as having a true stomach epithelium.

There was no evidence in the swollen canal part in any specimens examined, of the presence of tubular digestive, or pepsin, or gastric glands, with their specialized cells. Such glands are well described in Oppel, (1896, pp. 22, 33, 69). This lack, (point 1 of Pictet's summary) shows likewise that there is no specialized stomach part present in *Campostoma*.

Most of the evidence demonstrates lack of a true stomach in *Campostoma*, for, to summarize, there is a lack of a pyloric valve, a similarity of folds throughout in swollen part and back of bile duct junction, a similarity of epithelial cell structure in those parts, the presence of goblet cells throughout, and the absence of true stomach or gastric glands. Apparent contradictory points, the somewhat more posterior bile duct junction, and some acid reaction of the swollen part, are of less determining value, in comparison with the other positive structural features. Moreover bile duct junction need not be and often is not at the very beginning of an intestine. The fact that there is considerable distance anterior to it, allows room for the presence of acid reaction, which may not interfere with alkaline juices introduced farther down. By what means the acid secretion is produced is not known. But its presence, as long as not deleterious, does not seem remarkable when one considers that the absence of a stomach in this and other Cyprinidæ is probably not primitive, but rather a case of loss of an earlier physiologically differentiated stomach, which conclusion, entertained by Edinger (1876), seems logical when one realizes that most Teleosts have a true stomach. In Cyprinidæ the loss seems to be universal, but in some other groups there are only occasional species which lack a true stomach, (Oppel, 1896, p. 33). It is possible then that the loss is not equally complete in all cases, and that the slight indication of stomach acidity is a vestige in *Campostoma*.

All of the swollen part is therefore considered as part of the intestine in this paper, and all measurements of intestine length to be given are from posterior end of oesophagus to anus.

III. DEVELOPMENT OF THE INTESTINE.

The alimentary canal very likely begins as a straight tube, but this condition must be of very brief duration in post-embryonic life. The smallest fish obtained, 13 mm. long, already possessed the flattened Z-shaped canal.

Correlation of intestinal development with development of fish as a whole, though desirable, is impossible. Furthermore, since exact age records are not available for collected material, and thus correlation of intestinal development with age impossible, there remains merely the correlation between length of intestine and length of fish. While this is useful, it must be understood that no very close correlation is to be expected.

All specimens were assigned numbers, which are purely accession numbers, having no other significance. Length of fish is given in millimeters to base of tail.

A typical method of intestinal development obtains in by far the largest number of specimens. Definite detailed advances in this development are assumed to represent stages, designated as stage I, II, III, etc., which are figured on Plates I to V, inclusive.

Inasmuch as intestinal arrangement in the smallest available fish is similar to the general adult alimentary tract in many fishes, this study of development in *Campostoma* might in a way be considered a study of development of complex, coiled condition of a long-intestined fish, over the adult condition of a short-intestined carnivorous fish.

Stage I. (Plate I, Figs. 1, 2). The earliest stage of intestinal development has already been sufficiently described as a flattened Z-shape, of which the three sections, anterior, middle and posterior, are to be remembered as basis for the following developments.

Stage II. (Plate I, Figs. 3, 4). A little growth elongating the posterior canal section, results in a downward bend near the anterior end of that posterior section, at (b) in Fig. 3. This initial, downward U-shaped bend leaves in original position adjacent parts of that section, which now appear as upward bends (a) and (c). In subsequent intestinal coiling, curve (a) will persist as a characteristic landmark on the left side.

Stage III. (Plate I, Figs. 5, 6). Downward bend (b) is deeper. There has also been some growth in the middle section of the canal, where there is a slight bend, nearly in the horizontal plane.

Stage IV. (Plate I, Figs. 7-9). More elongation in the U-shaped bend (b) carries its rounded end across ventrally up to the right side. There is new development in the formation of a bend in the middle section, bend (d), which lies outwardly contiguous to or surrounds (b) ventrally, and there is likewise formed in it the bend (e) which pushes in directly inside of bend (c). All these bends are plainly seen in Fig. 8. The contiguous bends (b) and (d) comprise a double U-shaped bend, now already half way up on the right side, and it is this which will have to be followed primarily.

Stage V. (Plate I, Figs. 10-12). Growth carries bend (b-d) up higher on the right. The left side is as in the preceding stage, except that the posterior part, bend (c-e), is projected upward somewhat, so that it is level with the upper edge of the air bladder.

Stage VI. (Plate I, Figs. 13-15). There is no additional growth upward of (a) or (c-e) or of any other place on the left side. Probably nothing in growth processes of intestine itself would prevent growth in this direction, but the liver (Plate VII, Figs. 92, 93), offers mechanical obstruction. It occupies all available space anterior to and above bend (a) and anterior to (c), though not really above (c), and so could hardly be the cause of lack of growth from the left dorsalmost posterior to point (c). At any rate all subsequent growth of intestine results in elongation in the other direction, to the right or counterclockwise. At this stage there is but little apparent growth of (b-d), but enough to make these bends more posteriorly directed. At this time the anterior half of the anterior canal section begins to widen a little.

Stage VII. (Plate I, Figs. 16-18; Plate II, Fig. 22). The (b-d) bend has become more elongated posteriorly, with the end twisted around the tip of the air bladder. Fig. 16 shows the inner side of the tip of the (b-d) bend, stippled darker than the nearer left parts of intestine. The anterior canal section begins to elongate a trifle faster than the body as a whole, making a slight curvature in its course.

Stage VIII. (Plate I, Figs. 19-21; Plate II, Fig. 23). The distinctive development is the growth of the (b-d) bend so that for the first time it lies on the dorsal side of the air bladder.

Stage IX. (Plate II, Figs. 24-28). Continued growth of the (b-d) bend has carried it down half way on the left side so that the outer edge of (d) touches the posterior canal section. Thus the posterior part of the air bladder (Figs. 24, 25), is completely covered dorsally, except for a slit left in the loop of the (b-d) bend. Thus the first complete turn around the air bladder is completed.

The anterior canal section has elongated a little, forming a bend in its thinner posterior half, the end of which has passed from the ventral side, up the right, to the level of the upper part of the air bladder.

Stage X. (Plate II, Figs. 29-32). Bend (b-d) has grown over ventrally to the right side, a half a turn counterclockwise beyond stage IX.

The last part of the posterior intestine section, which had previously passed along the left side to the anus, has now elongated so that it passes ventrally, counterclockwise in a half turn to the right, on which side it passes along above the end of bend (b-d) to the anus.

The anterior section of the canal has grown a little, so that its posterior part has come to lie over the posterior tip of the air bladder, after which it continues into the middle canal section.

A small beginning is here formed of what will be later an inner series of coils. This inner, new intestinal bend may be partly visible in a view of the outer coils because it presses out into the open slit in the end of bend (b-d).

Stage XI. (Plate III, Figs. 33-41). The (b-d) bend has grown from the right, across the dorsal surface, and to the upper part of the left side. These new dorsal loops push forward the older loops which had previously covered the posterior part of the air bladder. Some coils tend to be pushed together much, and the first encircling coil at the anterior end is pushed beneath the edge of bend (c-e) on the left side.

The elongating end part of the posterior canal section has formed another half turn counterclockwise, to the left where it passes back to the anus. This part has made one complete counterclockwise turn between stages IX and XI.

The inner growth, seen only on removing outer posterior coils, is an elongation of the posterior part of the anterior section, and of a small adjacent part of the middle section. In most cases, from the position on the upper left margin, a new U-shaped bend, with the growing point indicated by (x), (Plate III, Fig. 38), makes half a turn counterclockwise. The extent of this is shown where intestine coils are unfolded in one plane, (Fig. 37), but in which all essential bends are retained. In a few cases the (x) growth is not quite as long (Fig. 39), and in a few cases (Figs. 40, 41) it has a different form due to different position of the part concerned relative to air bladder.

Stage XII. (Plate III, Figs. 42, 43; Plate IV, Figs. 44-54). The (b-d) bend has grown down from the upper part of the left, across ventrally to the right side. There is a little more crowding of coils anteriorly.

The end part of the posterior section has made another short diagonal bend around to the right side, where it passes to the anus. (Plate IV, Fig. 44). This has completed one full turn from stage X.

The growth of the inner coils is considerable, but there is much variation in the disposition of the (x) bend. Typically the (x) bend has passed from the right across dorsally, then down the left and across ventrally again. (Plate IV, Fig. 47). The (x) bend in growing around practically a full turn, has thus caught up with the (b-d) bend, but there is relatively no more growth, for its periphery is smaller than that of the older, outer bend. One loop of the (x) bend is usually visible in the small opening in the end of the (b-d) bend.

There were found many specimens of this stage with less growth in the inner part, due possibly to the retardative action of the pressure of the outer coils. Representative variations are shown, (Plate IV, Figs. 48-54). The inner growth in Fig. 49 has a crowding up of small loops which do not encircle the air bladder.

There is another peculiarity of coiling in some specimens. (Figs. 52-54). To distinguish this it should be recalled that in all intestinal development, as described, there was from the very first, a pushing around by elongation or growth of the U-shaped bend in a diagonal, spiral, counterclockwise direction. But in this peculiar type, there is a simple spiral turn around the air bladder, in one or a few counterclockwise turns. This condition may be brought about by the separation of the legs of the U at an early stage of the inner growth. A working model of wire and string, on a stick representing air bladder, disclosed how this could come about. Consider the condition in stage X in which the posterior part of the anterior canal section passes from the right across the posterior tip of the air bladder, to the middle intestinal bend. By a twisting or revolving of the anterior section just on this posterior point as a pivot, which is likely due to varying pressure on these parts, this simple spiral is produced during the course of the lengthening of the inner bend, instead of a U-shaped (x) bend being produced.

Not only fish of from 35 to 50 mm. length, but also most of the larger, older specimens, possessed coiling of this development stage XII. This is shown to be an adult condition. Even a few of stage XI intestinal development were adult, showing that the coiling may, but usually does not, stop at that point. In older specimens there is of course increase of actual intestine length, due to regular growth, in correlation with general increase of size of fish. That there is no relative increase of intestine length was seen in comparing ratios of intestine length to body length for all specimens of stage XII. Old large specimens were found to have the same range of ratios as younger ones which had just attained that development. This individual specimen comparison data cannot be given space in this paper. Table 2, summarizing all data, gives necessarily only averages for the series.

Stage XIII. (Plate IV, Fig. 55; Plate V, Figs. 56-59). There are instances in which more coiling does take place. As compared with 105 specimens of the collection which were in stage XII, 31 specimens had definite additional coiling, which also increased the ratio of intestinal length to body length (see table 2). The (b-d) growth has continued, passing up on the right side, and just across the tip of the dorsal side once more, or a half a turn more counterclockwise.

The end part of the posterior canal section likewise elongates, making another bend from the right, across the dorsal, and down diagonally on the left side to the anus. (Plate V, Figs. 56-58).

The inner growth also continues. From the right side, the (x) bend passes up and across the posterior tip of the air bladder, (Plate IV, Fig. 55). The same sort of variations of the inner coils exist as for stage XII.

Conclusion.—The development to stage XII or to XIII, is attained early within the first year of growth, often shortly after the middle of the summer, at which time stage XII fishes seem to average from 35 to 50 mm. in length. If stage XIII is developed this is done immediately without halt. Subsequent to this first summer's intestinal development to either of these stages, there is no further change, except the increase in length and thickness of intestine correlated roughly with increase in size of fish as a whole.

TABLE 1.

Data on specimens selected for illustration of stages in development of intestine.

Stage of Development	Specimen No.	Length of Fish, mm.	Length of Intestine, mm.	Number of times Intestine is longer than Body
I	296	14	12.6	.90
II	299	13	13.1	1.01
III	365	16	18	1.12
IV	314	16	18	1.20
V	367	18.5	29	1.52
VI	383	24	46	1.92
VII	401	26	57	2.19
VIII	396	25	63	2.52
IX	422	28	79	2.82
X	522	36	115	3.19
XI	195	41	165	4.04
XII	151	48	271	5.64
XIII	123	49	293	6.04

Relative to the largest specimens studied, the following data apply directly to the conclusions here made. Of five specimens over 100 mm. in length, (100 to 110 mm.), only two, (100 mm. and 102 mm.) had intestinal development of stage XIII; the others were stage XII. Of four specimens between 90 and 100 mm. in length, none were of stage XIII, all being stage XII. All these were old specimens. It may be mentioned, of course, that none of the specimens secured were of maximum

size the species may attain, but since the development process as far as degree of coiling is concerned, ceases so very early, this would be of no importance. Among the total of 31 specimens of stage XIII, there were also a number of small ones, one at 34 mm., one 43 mm., one 49 mm., and at almost all sizes upward to large, old fish.

TABLE 2.

Summary of measurements of specimens arranged according to stages of intestinal development.

Stage of intestinal development	Total number of specimens	Minimum length of fish, mm.	Maximum length of fish, mm.	Average length of fish, mm.	Minimum length of intestine, mm.	Maximum length of intestine, mm.	Average length of intestine, mm.	Minimum ratio ⁴	Maximum ratio	Average ratio ⁵
I.....	5	13	15	14.2	12	13	12.6	.87	.93	.90
II.....	2	13	13	13	12.1	13.1	12.6	.93	1.91	.97
III.....	3	14	16	15.3	15	18	16.3	1.00	1.12	1.06
IV.....	32	15	19	16.1	17	24	19.9	1.13	1.44	1.24
V.....	29	17	23	19.5	14	34	28.6	1.30	1.67	1.47
VI.....	28	19	61	25.4	31	107	38.8	1.55	1.96	1.53
VII.....	21	22	39	27.2	38	68	55.0	1.65	2.26	2.02
VIII.....	26	24	55	27.8	53	87	65.2	2.14	2.60	2.34
IX.....	47	20	73	33.0	53	108	88.8	2.31	3.34	2.69
X.....	65	21	81	36.1	75	270	116.3	2.59	3.57	3.22
XI.....	149	22	98	44.1	81	378	180.0	3.21	5.38	4.09
XII.....	105	32	110	59.1	160	614	296.7	4.28	5.90	5.02
XIII.....	31	34	102	68.1	210	794	488.2	5.77	7.94	6.58

Increase in intestinal development then has meant the gradual acquirement in the first half year of life, of a relatively long intestine, as seen in the regular increase in ratios between intestine and fish lengths for successive stages of this development. (Table 2).

⁴The minimum (or maximum) ratios are not to be understood as belonging to the particular minimum (or maximum) lengths of fish, in any stage. Body lengths, intestinal lengths, and ratios, are independent in that sense. Small young fish, say of stage XII, have the same range of ratios as large old ones, of same stage. For instance, in stage XIII, the smallest fish (34 mm.), has a ratio of 6.17, and the largest fish (102 mm.), has a ratio of 6.58, both fairly near the average. Sometimes smallest fish happened to have unusually high ratios. In stage XII, the very smallest fish (32 mm.), has ratio 5.90, the maximum found for that stage, while the largest fish (110 mm.) has a ratio 5.53.

⁵The average ratio (and similarly for all average lengths given) is the actual average of all individuals in the stage, not merely between the minimum and maximum specimens.

If one expects less range in ratios for a stage, with no overlapping of those of successive stages, assuming that for each fish length the intestine lengths in one stage of development ought to be the same, it must be recalled that such close correlation cannot be expected. Length may either outstrip or fall behind growth or development of intestine. Amount of available food of proper sort must be a factor determining increase in length and bulk. In a few specimens, of average normal size, from a small creek collection early in summer, there was almost no increase in length after being kept in an aquarium for two months. Out in nature the growth was continuous and considerable during the same time, as shown by measurements of average size fishes at later collections. Nevertheless in these stunted aquarium specimens, of which, however, only two survived until this point was investigated, intestinal development had continued to quite the normal advanced stage.

Another matter of practical importance in overlapping of ratios, is the fact that many specimens are naturally somewhat intermediate in development, that is, between successive stages. All things considered the correlation is as high as could be reasonably expected, and the increase in relative intestine length is regular.

If all adult specimens be compared a considerable range in ratios would be noted. Forbes and Richardson (1920, p. 111), say: "Intestine 5 to 9.5 times length of head and body." Others have given similar figures. The present work shows that all fishes of stage XII yield the average ratio 5.02. Since the general ratio does not increase for older, larger fish in this stage, the figure might do for adults, and numerous adults could be selected from the collections in which the intestine would be no longer than five times the body length. For stage XIII, where maximum intestinal length has been developed, the number of times the intestine is longer than the body ranges from 5.77 to 7.94, with an average of 6.58, but only seven out of 31 specimens had an intestine over seven times the length of the body.

IV. VARIATIONS IN INTESTINAL COILING.

A small proportion of *Campostoma anomalum* show marked variation from the described, typical intestinal development. Minute deviations are not counted in as variations. Out of 543 specimens of table 2, 103 could be differentiated at least in

some details of the outer coiling, but these cannot be of the least significance and they allow the specimens to be placed in a regular stage of intestinal development. Some (Plate VI, Figs. 68, 69), differ in appearance, due to slightly altered bends on the left side. In a few (Plate VI, Figs. 70, 72, 75), the dorsal side of the air bladder is not wholly covered posteriorly.

Some show so much variation that they cannot be homologized with the typical development. Most irregulars were characterized by absence of dorsal intestinal coiling, a noteworthy feature, in view of the usual coiling dorsally around air bladder. Out of 41 irregulars, 29 lacked all dorsal coiling, and were at same time old and large enough to have had it developed, were they typical. Only four very irregular specimens had some dorsal coiling, but they were otherwise so different as to have no similarity to the typical kind. The remaining 8 of the 41 were young, and naturally also without dorsal coiling, but they were so irregular otherwise that no direct comparison could be made with typical young. Apparently cases of irregular coiling begin very early in intestinal growth.

A number of specimens lacking dorsal coiling are figured, (Plate V, Fig. 63; Plate VI, Figs. 82, 87). The coiling, covering all other sides, has all main loops longitudinal, and this includes small subsidiary bends in the main longitudinal loops, chiefly on the ventral side. (Plate V, Fig. 61; Plate VI, Figs. 71, 80, 85). The left side shows in most cases long, sweeping bends, (Plate V, Figs. 60, 66; Plate VI, Figs. 79, 83, 84), and rarely a more straightened arrangement, (Fig. 76). The right side has in many cases two longitudinal coils, but one smaller than the other, (Plate V, Fig. 62; Plate VI, Fig. 81). The peculiar nature of this irregular coiling is best seen in view (Plate V, Fig. 64), of the entire turns flattened out as in (Plate IV, Fig. 46), with all essential bends retained. One of the very young of irregular type is similarly shown, (Plate V, Fig. 65).

The lack of dorsal coiling, though exceptional, is frequent and striking enough, so that one cannot safely make dorsal coiling around air bladder the main diagnostic test for the genus, as is done in most classification keys. In *Pimephales promelas* there is an arrangement markedly similar to many of these irregular *Campostoma*. The typical, transverse *Campostoma* coiling is probably a specialized condition, and its

absence may be thought of as a departure from the specialized method of the genus to a more generalized, earlier type of long intestine coiling.

On the basis chiefly of alimentary canal differences, Haseman (1906, p. 161) described a new species, *Campostoma brevis*. He compared an 81.5 mm. *C. anomalum* with an 83 mm. cotype of *C. brevis*. Measurements and descriptive details differ only minutely, having no significance and occurring within the range of variation of *C. anomalum*, but one distinct difference is an intestine in *brevis* scarcely half as long as in *anomalum*. His would yield a ratio of 4.41, intestine to body length, for *anomalum* as compared with 1.83 for *brevis*. Probably he did not measure in the apparent stomach, which would raise the *brevis* ratio well above two.

The writer found no 82 mm. or similar *anomalum* with nearly so short an intestine as in this *brevis*. All those lacking dorsal coiling had somewhat shorter intestine than typical ones of same size, but the difference was usually small.

There are other respects in which intestine of my irregular specimens, is either like the described *brevis*, or even more different than it, from typical *anomalum*. The writer would not consider making a new species for even the most irregular intestine type. Many of these in fact were found closely associated with a group of those shown to have regular coiled intestine, so that they must have belonged to the same school of young.

He gives among other intestine features, a diameter of 1.5 to 2 mm. for *brevis*, compared with 1 mm. for *anomalum*. The latter have a 1 mm. diameter average for such size fishes (omitting of course the swollen part). But one specimen, 74 mm. long, (Plate VI, Fig. 86), has intestines fully 2 mm. thick throughout. This intestine appears very short, but still having a ratio of 2.66, is longer than that of the described *brevis*.

Haseman says: "The alimentary canal of *brevis* does not go around the air bladder more than one or two times; and the other folds are not spiral, but longitudinal." The specimen referred to (Fig. 86), like *brevis* in its thick canal, does not have even one coil around the air bladder; and a total of 29 irregular specimens lack all dorsal coiling, and have it entirely longitudinal. A sort of intermediate specimen, (Plate VI, Fig. 70),

has merely a few coils around; however it has a very long intestine.

He described for *brevis* a white intestine, less fragile than the dark one of *anomalum*. *Anomalum* intestine is a dark, greenish brown in color, but several nearly white intestines were found, which was due to their possessing a much thicker wall. (Plate V, Fig. 66, was one of these). They were among those lacking all dorsal coiling, but the intestine was of small diameter and great length. He calls *anomalum* a mud-eater, and says *brevis* also has some "grassy substance" in its canal. *Anomalum* contents are mixed inorganic and organic matter, the latter largely diatoms, but there may be more or less green matter. (Kraatz, 1923). A very few had fed on green algæ exclusively, but they were darker, not lighter, and more fragile, rather than less.

While no positive statement can be made, the discussion shows that various more or less irregular specimens of *C. anomalum* show one or more of the various distinguishing *C. brevis* features, and that all sorts of variations and gradations occur, so that there seems insufficient basis, even with so short an intestine, for a new species.⁶

V. RELATION OF INTESTINE TO ADJACENT STRUCTURES.

Liver.

The liver is large, filling up space adjacent to the anterior parts of the intestinal mass.

On the left in all specimens, (Plate VII, Fig. 92), liver occupies all space in front of the most anterior, inverted, U-shaped bend of the intestine, and dorsal to it, and also in front of the double-U-shaped bend (c-e). In a few cases it does not extend as far back. The liver is rounded off anteriorly. From this large left lobe a narrow flat lobe extends and attenuates posteriorly, beneath the intestinal coils, which, as they develop around it, press grooves upon this liver lobe.

The large liver mass continues around ventrally and up the right side (Fig. 93), filling the larger space there, formed by the intestinal loops passing from the left diagonally and therefore more posteriorly to the right. From this large right lobe a thin

⁶Mr. Carl L. Hubbs, who subsequently examined *C. brevis* types, says it does not form a new species.

lobe extends tongue-like posteriorly, describing a long spiral of more than half a turn counter clockwise around the air bladder, and completely covered up by intestinal coils.

There are some variations in size and arrangement of liver, but these can be of no significance, and are dependent upon variations in arrangement of intestinal loops. Only the typical form has been figured.

Gall Bladder.

The gall bladder is a small dorsal sac appended to the alimentary canal by a fine duct, somewhat behind the middle of the anterior canal section. The point of junction is not always in relatively the same place. The sac folds down anteriorly, is covered with fatty tissue, but is not embedded in liver. It is shown in practically normal position, (Plate VII, Fig. 89), with the ducts slightly raised. The other illustrations (Figs. 88, 90, 91), show it swung up free from the canal, in Fig. 88 up around to the right of the ducts. The gall bladder is practically always of very similar form and fairly uniform size.

The cystic duct is short and straight, and about one-third the length of the bladder itself. The common bile duct or choledochal duct is three times as long as the cystic duct. Its lower part is rather close to and parallel to the intestine, and the exact place of entrance is rather hard to make out. It is not dorsal but on the left side.

The hepatic ducts were not studied much. Either one duct or two ducts come off from the common bile duct and diverge from the cystic duct. Wherever there was but one this soon divided into two branches, which entered the liver, apparently the right lobe, which extends around the air bladder. In rare cases three hepatic ducts were seen to come off together at the cystic duct junction. Just within the liver tissue the hepatic ducts divide into a number of smaller branches.

Pancreas.

The pancreas is difficult to distinguish. The following account is merely a preliminary statement.

In a considerable number of specimens examined, a fine irregular diffuse tissue, arranged lengthwise on the dorsal side, on the posterior half of the intestinal canal section, seemed likely to be pancreas. No ducts were found leading into

intestine, but under low power of the microscope some specimens showed masses of finely branched lobulated tissue with some fine tubules. Such a diffuse condition would not be unusual for fish pancreas.

It is also possible that pancreatic tissue may be included in liver, so that this organ would be an hepato-pancreas, which is not unusual in fishes. Oppel (1896, p. 42), gives, after Krukenberg, (1882), in a table of distribution of digestive glands and enzymes, an hepato-pancreas present for all Cyprinidæ.

The striking variability in condition of pancreas among fishes is well stated by Kerr (1919, Vol. II, p. 190). About *Campostoma* no conclusion can naturally be made without an extensive study histologically of pancreas and liver.

Gonads.

The gonads lie dorsal to the coiled intestinal mass, and are not enclosed in the coils, though it has been said, (Jordan and Evermann, 1896, p. 294): "ovaries similarly enclosed by the alimentary canal." If the oviduct were enclosed it would be compressed by intestinal coils, especially where there are both inner and outer coils, and most in later stages. Even anteriorly where there are no inner loops, the intestine presses upon the enclosed liver to make depressions upon it. It would seem impossible for an ovary to have room to develop within the coils anywhere.

Ovaries were observed in many specimens, but most were immature. Young specimens of not over 40 mm. (Plate VII, Fig. 98), had such immature ovaries. Nothing is known of rate of ovary development. A few specimens considerably larger and further developed in other organs, possessed, nevertheless, an ovary of small size, (Fig. 99). An older ovary (Fig. 100), fills up more space laterally and dorsally to the anterior half of the intestinal mass, including available space above the air bladder not filled by intestine. In this condition the two ovaries were found to be identical, and nearly touched along the median dorsal line.

In much older specimens the ovary is considerably larger, (Plate VII, Figs. 101, 102). These figures show the largest specimen at hand having a much larger ovary than in above-described stages. Only one other specimen, (smaller in size), had what seemed a fully developed ovary, and it was exactly

like the other, so that the one here treated of seems likely to be a normal adult form of ovary.

In this the ovary covers most of the intestinal mass on the left side. Only the inverted U-shaped bends are exposed anteriorly, and it extends in somewhat beneath these, (Fig. 102). The ovaries have lost symmetry, and are not bilaterally placed. The right is larger and has somehow come to be placed dorsally. It also extends down on the left, its lower margin making a diagonal line passing to the ventral side at the posterior end. Only at the anterior end above the liver, does the right ovary occupy the right side. Why the right ovary should not pass backward on the right over intestine is not clear, since it does push over dorsally and down the left side. The left lobe is smaller. Its upper margin adjoins the lower margin of the right ovary, (Fig. 101). It is pushed somewhat ventrally by the right one, but does not extend farther than the mid-ventral line.

VI. SUMMARY.

Campostoma anomalum normally has its air bladder (except dorsally at anterior end) encircled by many loops of a transversely coiled intestine, a feature found only in this genus of fishes.

The species is similar in most essential respects to other Cyprinidæ, in lacking a true functional stomach, a conclusion based on various features of canal structure different from those of Teleosts, having a true stomach.

The mucosa lining bears zig-zag, lengthwise folds. The zig-zag ridges are comprised of columns of Vs, which become smaller posteriorly. Farther back parts of the Vs disappear, merely short ridge pieces remaining, while at the end all folds are lacking.

In the very young fish, the canal, between oesophagus and anus, consists of three straight portions (anterior, middle, posterior), in a flattened Z shape. The anterior swollen portion is the apparent stomach.

Adult intestinal condition is the result of regular increase of coiling during the first year of growth. The first growth, a U-shaped bend, at anterior end of posterior canal section, plus another bend in the middle canal section, form a double U, the elongation of the rounded end of which, pushing counter clock-

wise around the air bladder, produces most of the intestinal coiling. Either two and one-half or sometimes three complete turns occur. There is a similar, shorter inner growth at the end of the anterior canal section, and also a lengthening of the posterior section by simple spiral growth.

The number of times the intestine is longer than the body increases with the stage of development. In many developed specimens it is 5 times, and in some few 6 and even more than 7 times the length of the body.

There are some irregular specimens, (one-fourteenth of all those studied) which for the most part lack all dorsal coiling and are thus very atypical in intestinal plan.

The liver occupies available space anteriorly in the abdominal cavity, and has thin lobes extending posteriorly, which are covered by intestinal coils. The gall bladder is a dorsal sac attached somewhat behind the middle of the anterior canal section.

The ovaries are not enclosed by the coiled intestinal canal, but lie directly upon it.

EXPLANATION OF PLATES.

All Figures illustrating intestinal development (Plates I-V), show alimentary canal posterior to oesophagus, and include also the air bladder. So as not to obstruct clear view of intestinal coils, all liver, mesentery, fat, gonads, etc., are omitted. Fine, parallel lines indicate air bladder, distinguishing it from intestine which is stippled.

PLATE I.

All Figures $\times 2$ & $2/3$.

- Fig. 1. Stage I, left view, specimen No. 296, length 14 mm.
- Fig. 2. Stage I, ventral view, specimen No. 296, length 14 mm.
- Fig. 3. Stage II, left view, specimen No. 299, length 13 mm.
- Fig. 4. Stage II, ventral view, specimen No. 299, length 13 mm.
- Fig. 5. Stage III, left view, specimen No. 365, length 16 mm.
- Fig. 6. Stage III, ventral view, specimen No. 365, length 16 mm.
- Fig. 7. Stage IV, left view, specimen No. 314, length 16 mm.
- Fig. 8. Stage IV, ventral view, specimen No. 314, length 16 mm.
- Fig. 9. Stage IV, right view, specimen No. 314, length 16 mm.
- Fig. 10. Stage V, left view, specimen No. 367, length 18.5 mm.
- Fig. 11. Stage V, ventral view, specimen No. 367, length 18.5 mm.
- Fig. 12. Stage V, right view, specimen No. 367, length 18.5 mm.
- Fig. 13. Stage VI, left view, specimen No. 383, length 24 mm.
- Fig. 14. Stage VI, ventral view, specimen No. 383, length 24 mm.
- Fig. 15. Stage VI, right view, specimen No. 383, length 24 mm.
- Fig. 16. Stage VII, left view, specimen No. 401, length 26 mm.
- Fig. 17. Stage VII, ventral view, specimen No. 401, length 26 mm.
- Fig. 18. Stage VII, right view, specimen No. 401, length 26 mm.
- Fig. 19. Stage VIII, left view, specimen No. 396, length 25 mm.
- Fig. 20. Stage VIII, ventral view, specimen No. 396, length 25 mm.
- Fig. 21. Stage VIII, right view, specimen No. 396, length 25 mm.

PLATE II.

All Figures $\times 2$ & $2/3$.

- Fig. 22. Stage VII, dorsal view, specimen No. 401, length 26 mm.
Fig. 23. Stage VIII, dorsal view, specimen No. 396, length 25 mm.
Fig. 24. Stage IX, dorsal view, specimen No. 422, length 28 mm.
Fig. 25. Stage IX, left view, specimen No. 422, length 28 mm.
Fig. 26. Stage IX, ventral view, specimen No. 422, length 28 mm.
Fig. 27. Stage IX, right view, specimen No. 422, length 28 mm.
Fig. 28. Stage IX, spread out flat, specimen No. 422, length 28 mm.
Fig. 29. Stage X, left view, specimen No. 522, length 37 mm.
Fig. 30. Stage X, ventral view, specimen No. 522, length 37 mm.
Fig. 31. Stage X, right view, specimen No. 522, length 37 mm.
Fig. 32. Stage X, dorsal view, specimen No. 522, length 37 mm.

PLATE III.

All Figures $\times 2$.

- Fig. 33. Stage XI, left view, specimen No. 195, length 41 mm.
Fig. 34. Stage XI, ventral view, specimen No. 195, length 41 mm.
Fig. 35. Stage XI, dorsal view, specimen No. 195, length 41 mm.
Fig. 36. Stage XI, right view, specimen No. 195, length 41 mm.
Fig. 37. Stage XI, spread out flat, specimen No. 195, length 41 mm.
Fig. 38. Stage XI, inner coils only, specimen No. 195, length 41 mm.
Fig. 39. Stage XI, variation inner coil, specimen No. 485, length 39 mm.
Fig. 40. Stage XI, variation inner coil, specimen No. 133, length 37 mm.
Fig. 41. Stage XI, variation inner coil, specimen No. 589, length 30 mm.
Fig. 42. Stage XII, left view, specimen No. 151, length 48 mm.
Fig. 43. Stage XII, ventral view, specimen No. 151, length 48 mm.

PLATE IV.

All Figures $\times 2$.

- Fig. 44. Stage XII, right view, specimen No. 151, length 48 mm.
Fig. 45. Stage XII, dorsal view, specimen No. 151, length 48 mm.
Fig. 46. Stage XII, spread out flat, specimen No. 151, length 48 mm.
Fig. 47. Stage XII, inner coils, specimen No. 151, length 48 mm.
Fig. 48. Stage XII, variation inner coil, specimen No. 238, length 44 mm.
Fig. 49. Stage XII, variation inner coil, specimen No. 206, length 50 mm.
Fig. 50. Stage XII, variation inner coil, specimen No. 594, length 39 mm.
Fig. 51. Stage XII, variation inner coil, specimen No. 597, length 36 mm.
Fig. 52. Stage XII, variation inner coil, specimen No. 17, length 41 mm.
Fig. 53. Stage XII, variation inner coil, specimen No. 221, length 54 mm.
Fig. 54. Stage XII, variation inner coil, specimen No. 583, length 36 mm.
Fig. 55. Stage XIII, inner coil, specimen No. 123, length 49 mm.

PLATE V.

All Figures $\times 2$.

- Fig. 56. Stage XIII, left view, specimen No. 123, length 49 mm.
Fig. 57. Stage XIII, ventral view, specimen No. 123, length 49 mm.
Fig. 58. Stage XIII, right view, specimen No. 123, length 49 mm.
Fig. 59. Stage XIII, dorsal view, specimen No. 123, length 49 mm.
Fig. 60. Irregular coiling, left view, specimen No. 58, length 42 mm.
Fig. 61. Irregular coiling, ventral view, specimen No. 58, length 42 mm.
Fig. 62. Irregular coiling, right view, specimen No. 58, length 42 mm.
Fig. 63. Irregular coiling, dorsal view, specimen No. 58, length 42 mm.
Fig. 64. Irregular coiling, spread out flat, specimen No. 58, length 42 mm.
Fig. 65. Irregular coiling, spread out flat, specimen No. 393, length 24 mm.
Fig. 66. Irregular coiling, left view, specimen No. 270, length 60 mm.

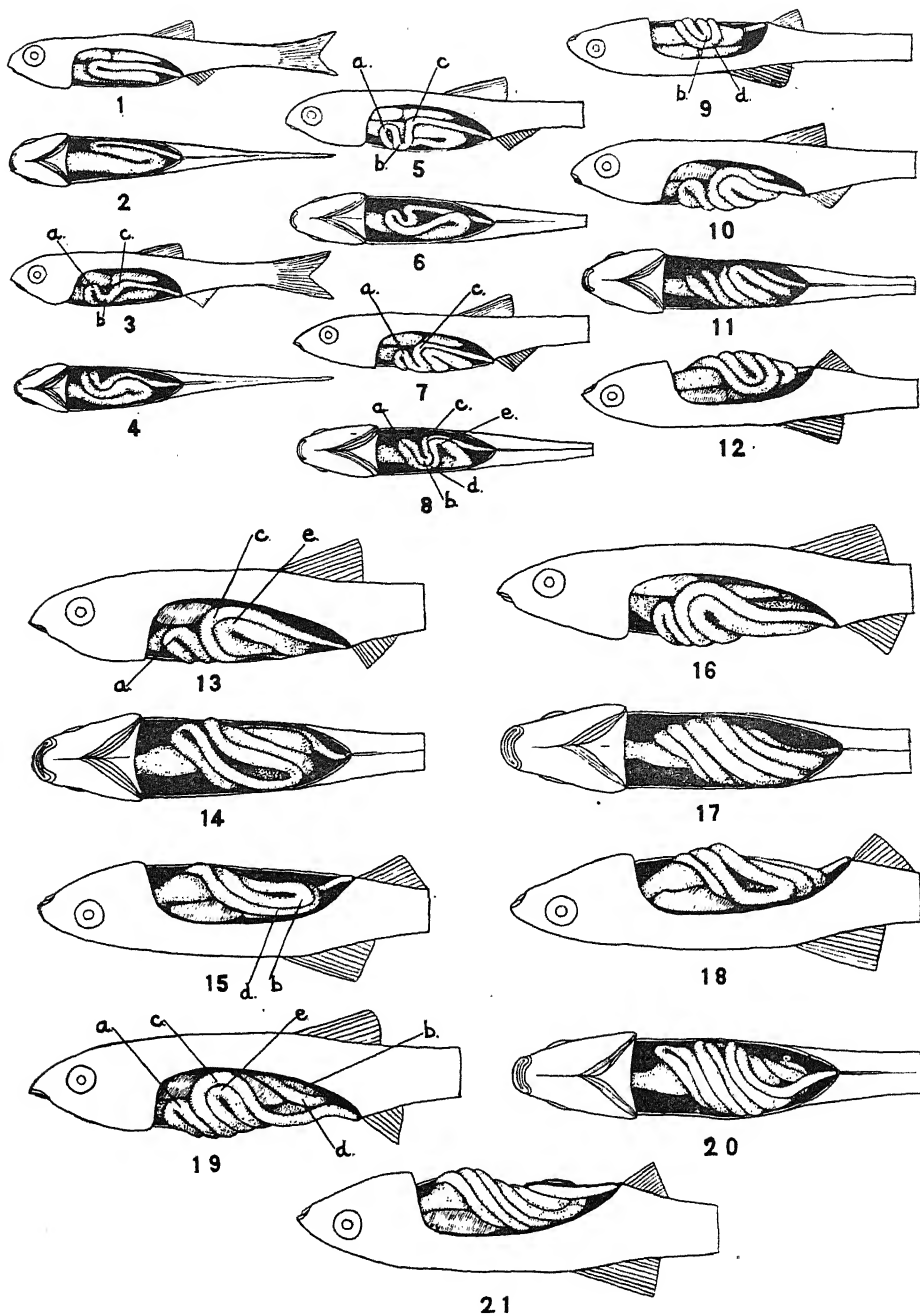
PLATE VI.

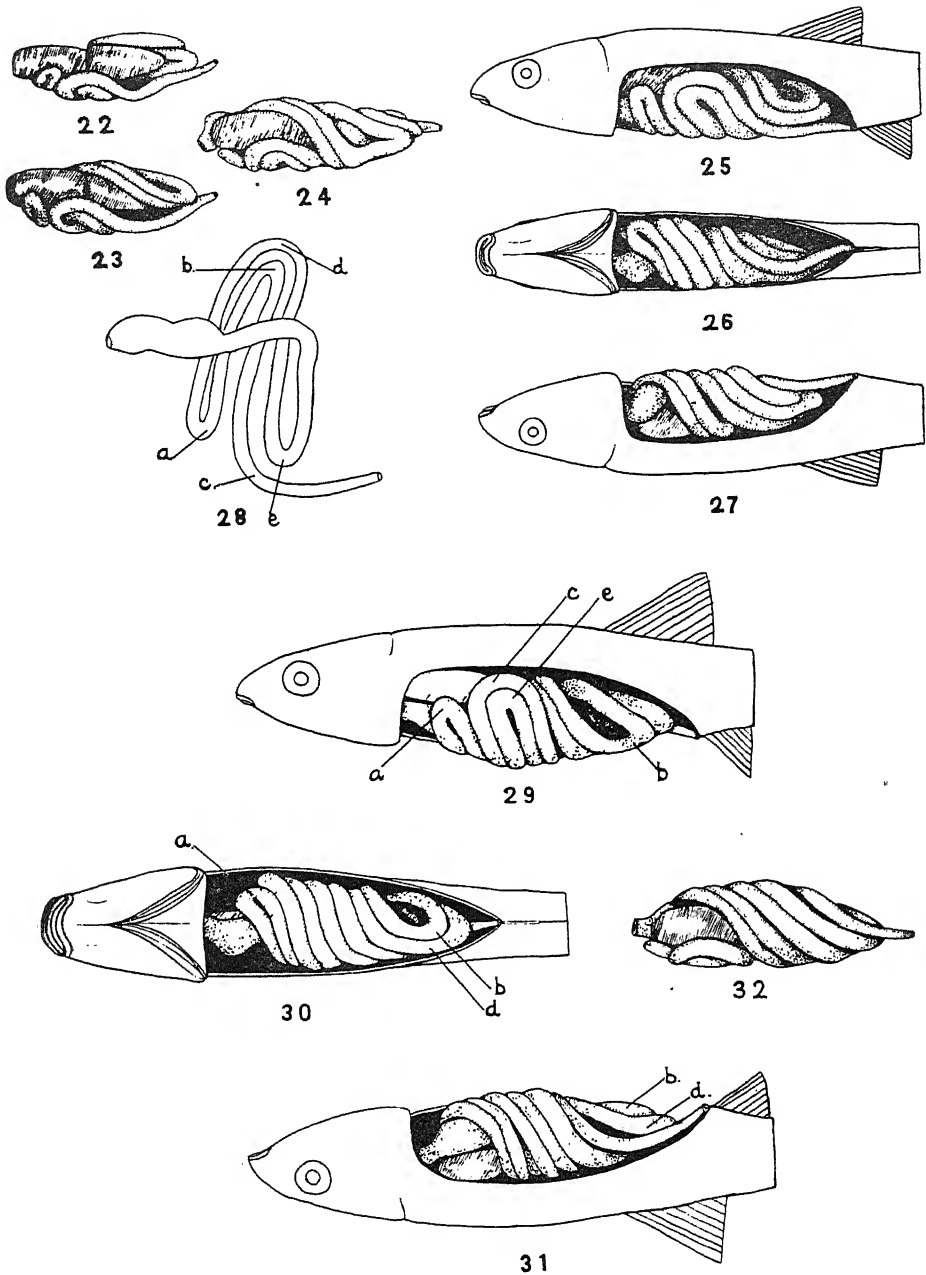
Photographs. All Figures $\times 1$.

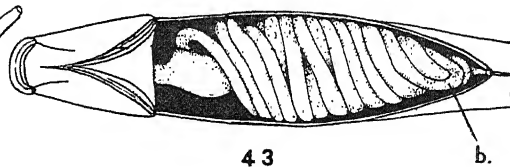
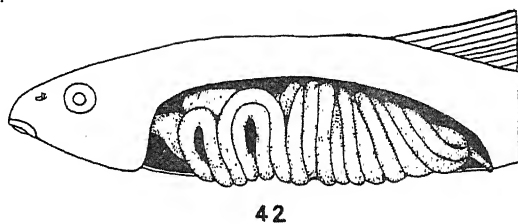
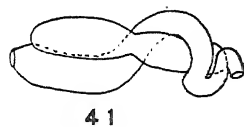
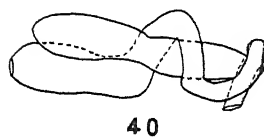
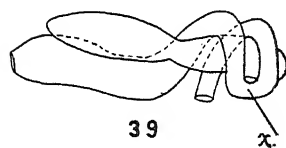
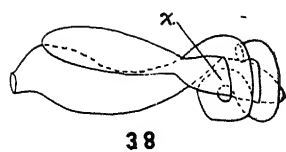
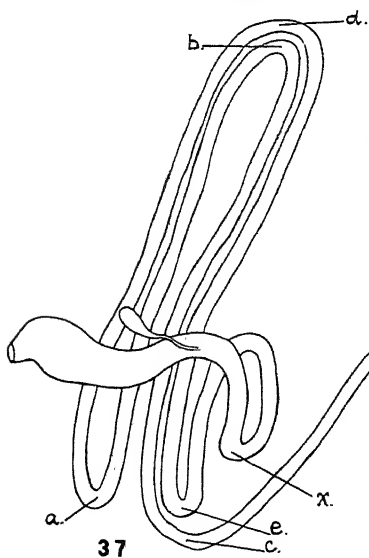
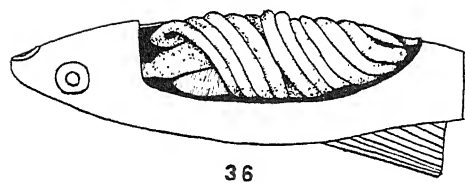
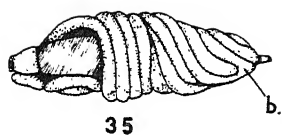
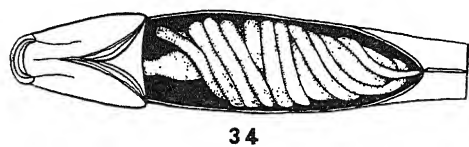
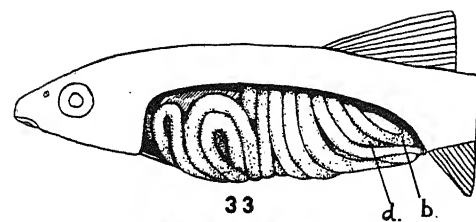
- Fig. 67. Typical coiling, left view, specimen No. 13, length 36 mm.
Fig. 68. Somewhat atypical, left view, specimen No. 252, length 100 mm.
Fig. 69. Somewhat atypical, ventral view, specimen No. 252, length 100 mm.
Fig. 70. Somewhat more atypical, left view, specimen No. 552, length 71 mm.
Fig. 71. Somewhat more atypical, ventral view, specimen No. 552, length 71 mm.
Fig. 72. Somewhat more atypical, left view, specimen No. 108, length 71 mm.
Fig. 73. Somewhat more atypical, ventral view, specimen No. 108, length 71 mm.
Fig. 74. Somewhat more atypical, right view, specimen No. 108, length 71 mm.
Fig. 75. Somewhat more atypical, dorsal view, specimen No. 108, length 71 mm.
Fig. 76. Irregular coiling, left view, specimen No. 572, length 59 mm.
Fig. 77. Irregular coiling, ventral view, specimen No. 214, length 86 mm.
Fig. 78. Irregular coiling, left view, specimen No. 51, length 66 mm.
Fig. 79. Irregular coiling, left view, specimen No. 111, length 57 mm.
Fig. 80. Irregular coiling, ventral view, specimen No. 111, length 57 mm.
Fig. 81. Irregular coiling, right view, specimen No. 111, length 57 mm.
Fig. 82. Irregular coiling, dorsal view, specimen No. 111, length 57 mm.
Fig. 83. Irregular coiling, left view, specimen No. 35, length 56 mm.
Fig. 84. Irregular coiling, left view, specimen No. 43, length 63 mm.
Fig. 85. Irregular coiling, ventral view, specimen No. 43, length 63 mm.
Fig. 86. Irregular coiling, left view, specimen No. 65, length 74 mm.
Fig. 87. Irregular coiling, dorsal view, specimen No. 65, length 74 mm.

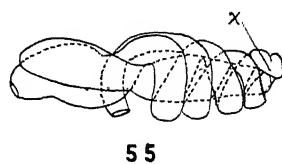
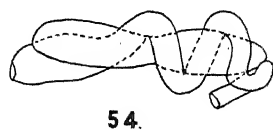
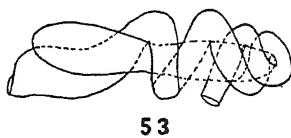
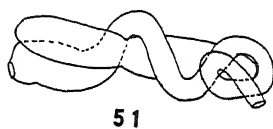
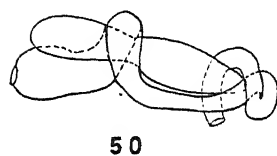
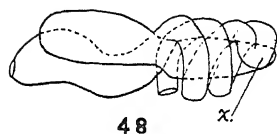
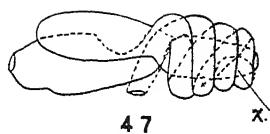
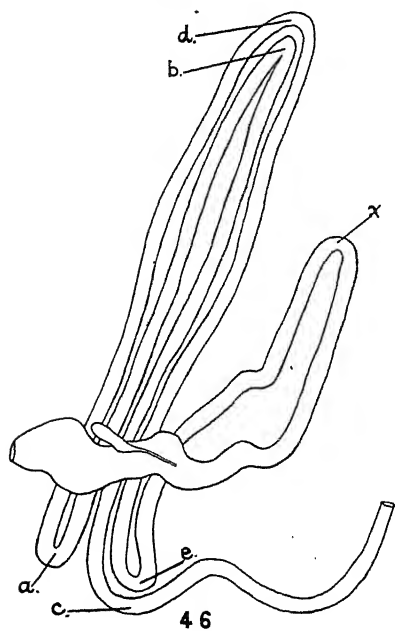
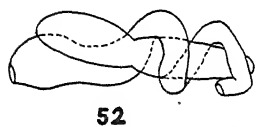
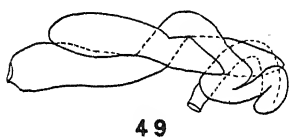
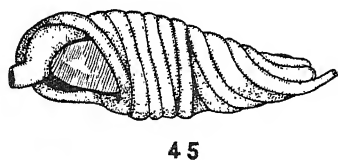
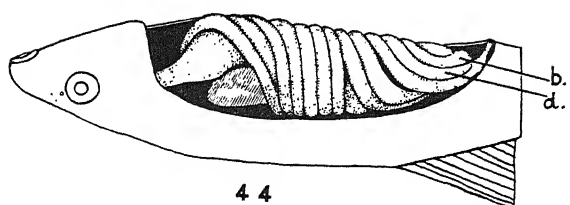
PLATE VII.

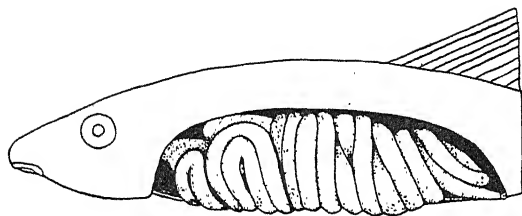
- Fig. 88. Gall bladder and ducts; Ga, gall bladder; Cy, cystic duct; He, hepatic ducts; Ch, choledochal or common bile duct. The gall bladder is lifted up dorsally. Specimen No. 48, length 36 mm. $\times 4$.
Fig. 89. Gall bladder and ducts; same fish but with bladder in natural position. $\times 4$.
Fig. 90. Gall bladder and ducts. Specimen No. 228, length 46 mm. $\times 4$.
Fig. 91. Gall bladder and ducts. Specimen No. 240, length 42 mm. $\times 4$.
Fig. 92. Liver, shown in relation to air bladder; no intestine shown; length 49 mm. Left view, $\times 2$.
Fig. 93. Liver, from same fish, right view, $\times 2$.
Fig. 94. Intestinal mucosa surface; anterior part of swollen region. Longest dimension of drawing is in circular surface of mucosa, spread out flat; shorter dimension is in direction of length of intestine. The grooves are shaded. Specimen No. 253, length 95 mm. $\times 6$.
Fig. 95. Intestinal mucosa surface; part of swollen region somewhat anterior to common bile duct junction. In same position and from same fish as Fig. 94. $\times 6$.
Fig. 96. Intestinal mucosa surface; farther posteriorly, about half way back to anus. Same position and from same fish as Fig. 95. $\times 6$.
Fig. 97. Intestinal mucosa surface; portion still farther posteriorly, about half way between Fig. 96 and anus. Same position and from same fish. $\times 6$.
Fig. 98. Ovary. Left side; specimen No. 25; length 39 mm. $\times 2$.
Fig. 99. Ovary. Left side; specimen No. 145; length 73 mm. $\times 2$.
Fig. 100. Ovary. Left side; specimen No. 276; length 58 mm. $\times 2$.
Fig. 101. Ovary. Left side; specimen No. 290; length 80 mm. $\times 2$.
Fig. 102. Ovary. Dorsal view, showing the right ovary; specimen No. 290; $\times 2$.







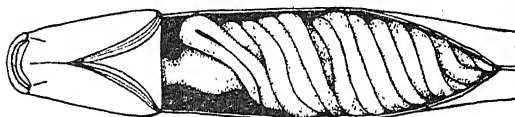




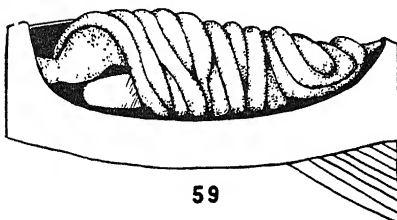
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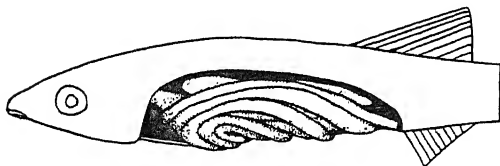
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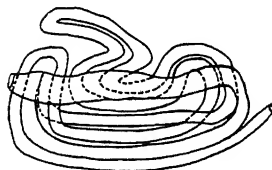
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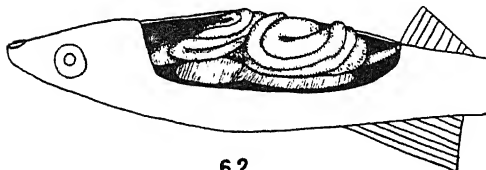
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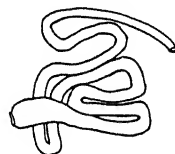
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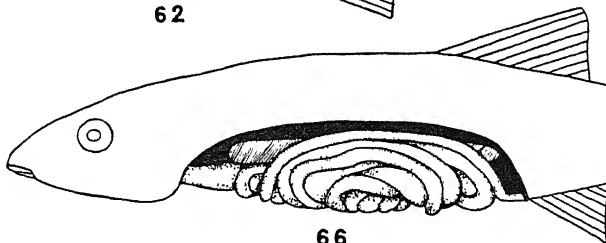
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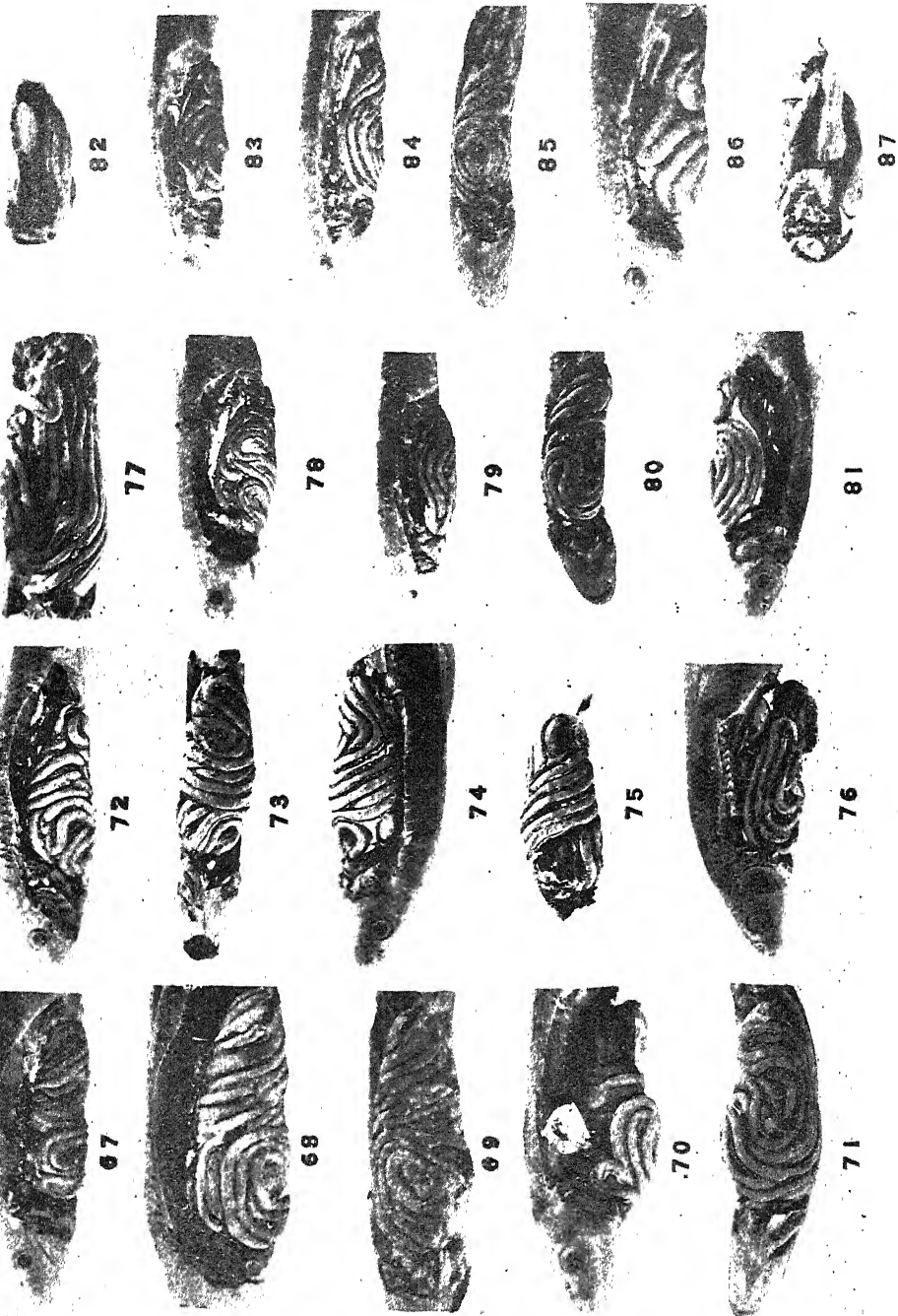
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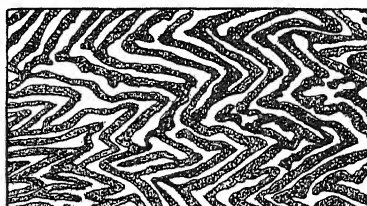
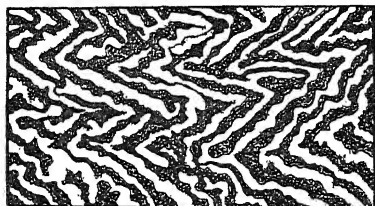
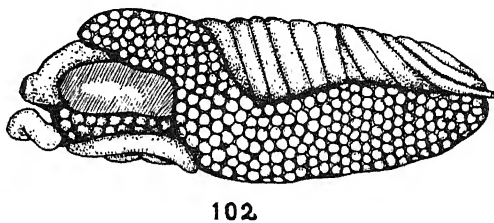
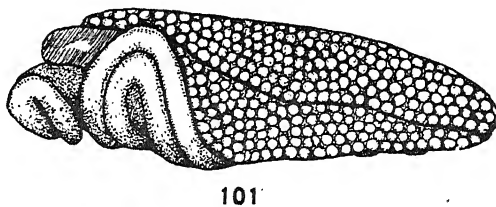
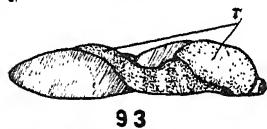
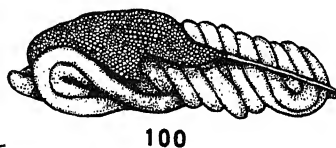
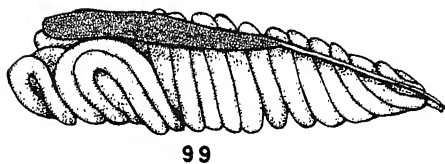
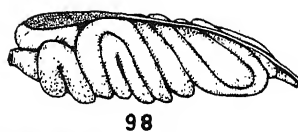
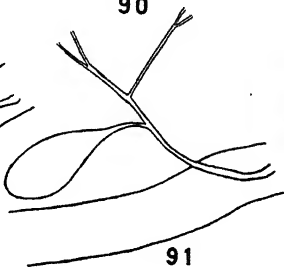
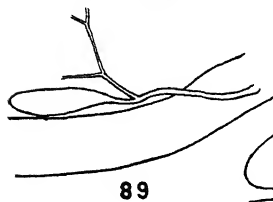
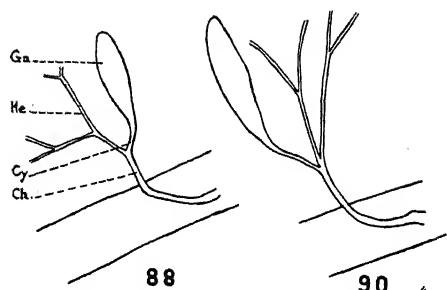


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CONDITIONS UNDER WHICH GONIOBASIS LIVESCENS OCCURS IN THE ISLAND REGION OF LAKE ERIE.*

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INTRODUCTION.

The distribution of *Goniobasis livescens* is so sharply defined in certain sections of the island region of Lake Erie and the situations in which it occurs are so varied in character that an examination into the factors involved naturally suggests itself. The conclusions offered here are based on observations recently made during several summers at the Lake Laboratory at Put-in-Bay. Quite a variety of conditions exists within the bay, and, because their proximity to each other made comparisons easy, the bay was carefully surveyed. This was followed by an examination of conditions throughout the island region. An attempt was then made to interpret the data in the light of a few simple experiments.

Much of the field work was done with the interested assistance of my wife and of a former student, Mr. E. L. Wickliff. I am also greatly indebted to Mr. Bryant Walker, who very kindly identified the snails.

OBSERVATIONAL DATA.

Put-in-Bay.

A rubble beach and a bar extending from it into Put-in-Bay at the latter's western extremity, both present sharp limits in the distribution of *Goniobasis*. The beach and one side of the bar are exposed to the lake; the opposite side of the bar faces the still water of a small cove.

The beach is composed of small stones, their size ranging from an average maximum of seventy-cubic inches to an average minimum of three cubic inches. They are washed constantly by waves which at times are quite severe. *Goniobasis*

*Contribution No. 77 from the Department of Zoology and Entomology, Ohio State University.

is practically absent. A few were found at one spot in ten inches of water on relatively large stones, i. e., averaging one hundred and sixty cubic inches. Just a few feet from this spot the beach makes a turn and faces the cove. In this undisturbed water, fourteen snails were collected from an area one foot square. They were at depths of two to four inches on stones averaging only eighteen cubic inches. Other animals found with them were the snail *Planorbis parvus* and the leech *Herpobdella punctata*. *Physa ancillaria* var. *magnalacustris** and parnid beetle adults and larvæ were also present but by no means as abundantly as on the exposed side of the beach.

The bar mentioned above is chiefly composed of small stones. The side facing the lake slopes gradually but the side toward the cove drops abruptly into deep water. *Goniobasis* was very scarce on the lakeward side. When found it was never in less than ten inches of water and it was always on the larger stones. Just around the free end, or nose, of the bar, where the lake waves could not be felt, the snails began to appear in less than ten inches of water on stones about forty cubic inches in size. Farther along, and distinctly on the cove side, specimens were common on the smallest stones, five or more to the linear foot. Some of them were barely covered with water. The portion of the bar nearest the beach is covered with one to two feet of water. Even here the snails are found on the coveward slope of the bar, where the force of waves from the lake is largely avoided.

Along the lakeward side of the bar, *Physa* was quite common and, in some spots, extremely abundant. Mayfly larvæ and caddis-worms were also present. On the cove side, none of these animals were as numerous, in fact the mayfly larvæ and the caddis-worms were decidedly scarce.

In this distribution the following points are clear: *Goniobasis* is more abundant in still water than in disturbed water; in the rough water they are on large stones or well beneath the surface, or both; in still places they are near the surface and may be on comparatively small stones.

These relations were compared with the conditions under which the snails occurred elsewhere in the bay. A few typical situations will be described.

*Wherever *Physa* is mentioned this species is meant.

In the cove, just discussed, there is a pile of stones on the island shore. One side of this pile is well protected, the other side is exposed to whatever force the waves have left after they sweep across the bar. On the protected side of the pile, in water two inches deep or less, the snails were abundant on stones averaging eighteen cubic inches. On the exposed side, the snails were not so numerous (twenty-two of them in an area one foot square) and those present, were on stones averaging thirty cubic inches.



A FAVORABLE HABITAT.

SQUAW HARBOR, a well protected section of Put-in-Bay. Pond conditions are approached. Clumps of reeds (*Scirpus*) and water lillies (*Nymphaea*) can be seen in the picture. There is an abundant growth of submerged plants such as *Potamogeton*, *Vallisneria* and *Myriophyllum*. The shore has been artificially faced with stones. *Goniobasis* is abundant among the stones near the surface.

Somewhat further along the shore of the bay, in a very well protected situation, there were one hundred twenty-nine snails in a square foot on stones four cubic inches in size, lying in four inches or less of water. By way of contrast, one may take a stretch of gradually sloping, stony beach, several hundred feet down the shore. The stones averaged four cubic inches and a small amount of sand was mixed with them. Upon occasion, this beach is swept by strong waves from the lake and, even on quiet days, there is a more or less constant ripple of water.

Goniobasis was occasionally seen in ten inches of water on larger stones, but not in water shallower than this. It is to be noted that *Physa* was fairly common and, therefore, the possibility that the sand acted upon *Goniobasis* unfavorably may be discounted.

A narrow channel cuts across the beach just described, into a small division of the bay called Terwilliger's Pond. At the entrance into this channel *Goniobasis* was present in two or three inches of water on stones one hundred to two hundred cubic inches in size, there being two or three snails on a stone. Individuals in this situation were exposed to waves from the lake and also to the sweep of a current, in and out of the pond, which at times became quite severe. One side of the channel is faced with the foundation beams of a bridge. On these, seven or eight snails occurred to a linear foot, often right at the surface of the water. The opposite side of the channel is bordered by an accumulation of small stones and, on these, *Goniobasis* was not found.

There is an indentation of the bay, known as Squaw Harbor, in which pond conditions are approached. It supports a rich growth of submerged vegetation, patches of reeds and pond lillies. The water is quiet even when the outer bay is considerably disturbed. The shore has been artificially faced with stone. *Goniobasis* is very commonly distributed along the shore. On the fine, silty mud of a well protected dike just within the entrance to Squaw Harbor there were approximately sixteen *Goniobasis* to a square foot in less than a foot of water. On the protected side of a gravelly point, at the entrance, fourteen of the snails were found in a square foot, but there were none on the opposite, exposed side.

The most common form found with *Goniobasis* on the stony shore of Squaw Harbor, was a freshwater sponge, *Spongilla* (sp?). *Planorbis trivolvis* and parnid beetle larvæ were less frequent and were found in about equal numbers. Crayfish, and the snails *Physa ancillaria*, *Planorbis parvus*, *Lymnaea humilis* were also present.

Extending across the entrance to Put-in-Bay is an island with a rocky shore. *Goniobasis* is decidedly scarce on the side facing the lake. When found it is a foot or more under the surface. It is abundant on a protected, stony bar extending from the island into the bay.

A detailed account of other parts of the bay would be essentially a repetition of what has already been given. In the bay, as a whole, *Goniobasis* was most abundant in protected situations. If present in exposed places, it was rarely less than a foot under the surface and, then, only on larger objects. When protected it was close to the surface on a variety of substrata.

The Island Region in General.

The distribution throughout the island region was taken up in the light of these observations. Certain critical areas were studied in detail.



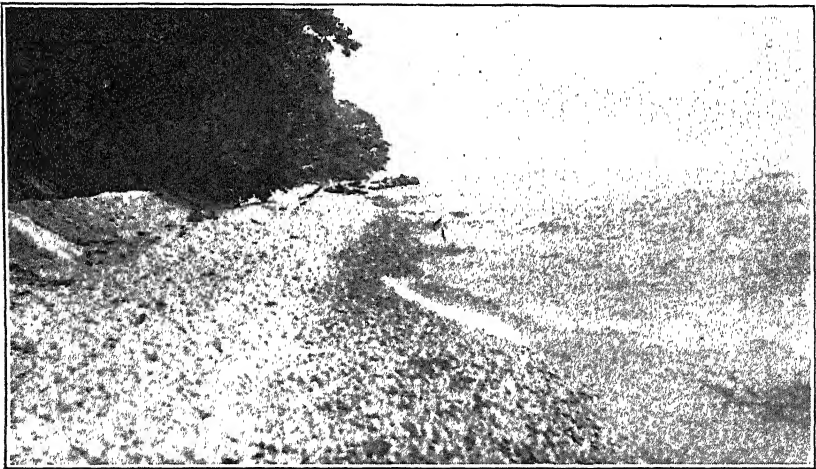
DIFFICULT CONDITIONS.

OLD HEN ISLAND, a fully exposed situation with rocky and bouldery shore. *Goniobasis* is scarce and when found it is usually 10 to 15 inches beneath the surface.

The eastern extremity of South Bass Island is a solid ledge of shelving rock, exposed to the full sweep of storms. On it, large boulders and smaller stones are scattered. A total of twenty *Goniobasis* was found here. They were taken, at different depths, in three different areas of a foot square. Accompanying forms were larvæ of stone flies, mayflies, caddis flies, parnid beetle larvæ, midge larvæ, a few *Physa ancillaria* and leeches. In calm weather, *Goniobasis* was distributed without much reference to the type of substratum. When the

water became rough, those found at the surface were restricted to the boulders and solid rock. The snails were found on smaller stones, only if the latter were ten or more inches under water, or else wedged firmly among larger objects near the surface. In extremely rough weather the snails passed to the protected sides of the boulders or to deeper water, in which case they were found on both large and small stones.

Near the southwest point of Middle Bass Island, on a fully exposed ledge of rock, *Goniobasis* was found only on the lower and, therefore, deeper parts of boulders. In four small areas



A VERY UNFAVORABLE SITUATION.

EAST SISTER ISLAND, a fully exposed rubble beach. *Goniobasis* was not found in such situations.

examined, only four *Goniobasis* were found, and these were in water two feet deep. Other forms on this ledge, usually in shallower water, were *Physa ancillaria*, *Lymnaea humilis* (most abundant), leeches, the larvæ of parnid beetles, caddis flies, mayflies and midges. All of them were common.

Ten miles to the north of Put-in-Bay, there is a group of four small islands, three of them hardly more than exposed ledges, known as the Hen and Chickens. On the Big Chicken, there is a ledge covered with stones and boulders. A few scattered *Goniobasis* were found on the boulders, none were on the stones. Along another side of the island, there were no large stones and

no *Goniobasis* were found. *Physa ancillaria* and the larvæ of caddis flies and mayflies, were quite common.

At the Old Hen, in rough water, the snails were scarce, even in fifteen inches of water and on stones having cubic dimensions of one hundred to two hundred and forty inches. In the protection of a dock, where the water is disturbed only in severe weather, and from but one direction, *Goniobasis* was very abundant at the surface on stones twelve to twenty cubic inches in size.

At West Harbor, on the mainland, five miles from South Bass Island, there is a sandy shoal. The sand is thrown into ridges and troughs parallel with the shore and at right angles to the waves. *Goniobasis* is quite common in the troughs, where the water is often waist deep. It is not found on the ridges unless the water is at least knee deep. The only other forms found in this habitat were the snails, *Pleurocera* (sp?) and *Campeloma* (sp?), an occasional midge larva and a few burrowing mayflies. .

Discussion.

The situations which have been described give a typical picture of the conditions in the island region. In general the habitats are similar to those described by other observers for other localities. That is, *Goniobasis livescens* is found on exposed, rocky shores and also in more protected situations. However, its relative abundance in these two types of environments in Lake Erie does not agree with certain reports for other localities. In Oneida Lake it is most abundant on exposed shores (F. C. Baker, '16). It is similarly reported for the Saginaw Bay region (H. B. Baker, '15), and for the Georgian Bay region (Robertson, '11). In Lake Erie it is most numerous in protected situations. In them, it is near the surface without much regard to the nature of the substratum. The relatively few individuals living in exposed places are usually found ten inches or more beneath the surface. When they are near the surface they are on a firm substratum; lower down they may be on smaller and less firmly placed objects.

EXPERIMENTS.

Any discussion of the factors involved in this distribution must consider the rather obvious correlation which exists between the wave action, the depth of the water and the nature

of the substratum. The possibility of variation in H-ion concentration or in carbon dioxide was taken into consideration, but no correlation was found to exist. Food was also considered as a factor but conditions in areas well inhabited by *Goniobasis* were similar to those in which it was less numerous.

Indirect Effect of Waves.

The two most obvious ways in which waves might influence snails, are either, indirectly, by moving the substratum, or directly, by moving the snails themselves. There is reason for thinking that both methods are operative. With regard to the first, it has been pointed out that the size and stability of the objects to which the snails were attached increased rather directly with exposure to wave action. A small stone is easily moved to and fro, a large one is not. With this in mind, a few simple experiments were performed.

I. A firmly wedged stone, one hundred twenty-six cubic inches in size, with a number of *Goniobasis* on it, was struck until it chipped. The stone did not move and none of the snails dropped off.

Another stone, two hundred sixteen inches in size, also firmly placed, was hammered for five minutes, the stone chipping in the process. It did not move. Only one snail out of ten dropped off and that one was near the spot being struck.

II. A stone, two hundred ten cubic inches in size, lying next to the stones of the first experiment but not firmly placed, was struck. The stone moved at the first tap and several snails on it dropped off. A stone, seventy-two inches in size, was tapped. Five snails were on it. The stone moved perceptibly. Three snails dropped off immediately and all were off at the end of thirty seconds.

A number of other tests, similar to the foregoing, were made. The results were uniformly the same. Whenever the stones were jarred sufficiently to cause their perceptible movement, the snails dropped.

Very evidently, an oscillatory movement of the substratum influences the snails in an unfavorable manner. And, in consequence, such a movement of the substratum brought about by wave action, must be considered as one of the factors, indeed, a very important factor controlling distribution.

Direct Effect of Waves.

This does not obviate the possibility that *Goniobasis* is influenced directly by the waves. Bearing upon such a possibility is the fact that the snails migrate vertically with changes in the degree of wave wash. When the water is quiet, or gently lapping, *Goniobasis* is a common object at the surface except where a gradually sloping substratum, in rather shallow water, tends to magnify the surface effects of small waves. As the water becomes markedly disturbed the snails move beneath the plane at which the waves break or, if the object to which they are attached is large enough to afford protection, they merely move around to the side opposite that from which the waves strike. However, it should be noted that the snails also do not leave these larger objects and, furthermore, that in troubled waters the snails are found only on the larger and more firmly placed objects for some distance below the surface, although they may not be in a protected situation when beneath a level where waves break.

This last fact serves to bring out the point that, in considering the direct effect of waves, a distinction must be made between the influence of the washing or breaking of waves, at the surface, and the subsurface wave motion. Individuals at the surface where waves break, receive a sudden blow on one side without anything commensurate to support them on the opposite side. Not only that, but they are frequently subjected to alternate blows on opposite sides in quick succession. The subsurface effect differs; there is water on all sides; the passage of the wave somewhat resembles a current. In the case of a current its full force may be just as severe as a blow delivered by a breaking wave, but its strength is usually gathered gradually and alterations in intensity take place in the same way. In this connection, it is worth noting that the snails on the foundation beams of the bridge, previously mentioned, did not change their position, when a current rushed by them with considerable force. This behavior is, of course, in line with the reaction of *Goniobasis* in streams. There it is frequently found on firmly placed stones in rapids. (Shelford, '13): The behavior also corresponds with what has just been mentioned, namely, that they remain on firmly placed stones beneath the surface, where waves sweep across them, but do not break.

A few simple experiments were tried to test the reaction of *Goniobasis* to movements of the shells, such as might be caused by water striking it.

I. Eight snails on a horizontal surface had the apex of the shell moved back and fourth through a distance of half a centimeter for five minutes. The snails reacted in two ways: they either began to glide over the stone or else they remained at rest and assumed a generally tense condition of the body, the latter being detected by the degree of resistance to the movements of the shell. These two modes of reaction sometimes alternated. Six of the snails stayed on the stone for five minutes; two of them dropped off at the end of two or three minutes. When the stone was moved by tapping, four of the snails fell off immediately and one dropped at the end of fifteen seconds.

II. Three snails, on a perpendicular surface, had their shells moved as in the preceding experiment. Two of them dropped off immediately and one remained for five minutes. Movements of the stone caused it to drop immediately.

III. Four snails, on a surface inclined 45° , were treated as in the two preceding cases. Two of them dropped off at once. One dropped at the end of thirty seconds. One remained for five minutes, at the end of which period, movement of the shell was stopped. When the stone was moved this snail dropped off.

IV. A number of snails were now tested to determine the effect of a sudden blow. Ten snails were struck suddenly, although as far as possible with no more violence than that of the oscillatory movement at its height. Eight snails dropped off at once and two of them fell at the second blow.

Discussion.

The results obtained from these experiments apply, of course, to the question of the movement of the substratum as well as to that dealing with the direct effect of wave action. It is clear that when both conditions are possible, an oscillation of the substratum is of more importance in determining the presence of *Goniobasis*, at a particular spot, than is an oscillatory movement of merely the shell and visceral mass. It is also clear that the snails do not maintain themselves against a sudden blow delivered to the shell. This is in agreement with what has been said regarding the effect of waves at the surface. And further, it is evident that the snails cling more readily to a horizontal surface than they do to a sharply inclined surface.

When we consider more in detail, why the snails should be so extremely sensitive to movements of the entire body caused by oscillations of the substratum and comparatively tolerant of movements due to the swinging back and forth of merely the visceral mass it is to be remembered that in snails the organ of equilibrium, i. e., the otocyst, is in the foot. Swaying of the substratum would thus stimulate this organ. It develops therefore, that *Goniobasis*' sense of equilibrium can be considered a factor of importance in the selection of a habitat.

With regard to the inability of *Goniobasis* to resist wave wash, the shape and size of its foot in respect to the shape and size of its shell is presumably a matter of importance. A comparison of the behavior of *Physa* and *Goniobasis* may be helpful in this connection. *Physa* lives where waves break and ripple, that is, in the very conditions which *Goniobasis* avoids. When one compares the morphological difference between these two snails, it is readily observable that the comparatively short and approximately square foot on *Goniobasis* coupled with its massive and prominently projecting shell must afford a poor holdfast, whereas, the long and slender foot of *Physa* coupled with its relatively low, rounded shell is a much better organ of attachment.

In connection with the fact that in Lake Erie *Goniobasis* is most abundant in protected habitats it should be noted that in streams it is typically a member of a rapids association. (Shelford, '13). In a body of water such as Lake Erie a rapids environment exists under conditions which *Goniobasis* can not readily tolerate. In a lake, a rapids environment is produced by the wash of waves; in a stream it is caused by a current. Waves deliver sudden, intermittent blows. These *Goniobasis* cannot withstand. Waves also cause an oscillation of movable stones. *Goniobasis* is sensitive to an oscillation of the substratum. The force of a current is relatively constant and alterations in strength are relatively gradual. *Goniobasis* can accommodate itself to such conditions.

The habitat preferences of *Goniobasis livescens* in the Lake Erie island region can thus be harmonized with the well known fact that it is a typical member of a rapids association in streams, by reason of the fact that the relatively constant current of a stream does not introduce the two disturbing factors of sudden blow or oscillating substratum.

SUMMARY.

In the Lake Erie island region *Goniobasis livescens* inhabits both exposed and protected situations. It is most numerous in protected places.

In general, the more exposed the habitat the larger the object to which the snails are attached or, within certain limits, the farther beneath the surface it is found.

With increasing degree of protection the snails are found nearer the surface and are distributed within the habitat with less regard to the nature of the substratum.

Wave action is the controlling factor in distribution. Its influence is felt in two ways: (a) directly by striking the snails, (b) indirectly by causing an oscillation of the substratum. Where both conditions are possible, experiments indicate that oscillation of the substratum is of the greater importance, apparently because such oscillation stimulates the organ of equilibrium.

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ADDITIONS TO THE LIST OF OHIO SPIDERS. I.

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The list of Spiders which follow is an addition to the list which was published in the Ohio Journal of Science, Vol XVIII, No. 8 in June 1918. It includes the nine new species described in the Ohio Journal of Science, Vol. XIX, No. 6, in April, 1919, as well as those already named, which have been found during the interval between June 1918 and June 1924.

DRASSIDÆ.

Drassylus frigidus (Banks).

♂ ♀ Rockbridge, Ohio, Sept. 30, 1917.

Drassylus rufulus (Banks).

♂ Rockbridge, Ohio, Oct. 4, 1914.

Haplodrassus signifer (C. Koch).

♀ Columbus, Ohio, May 25, 1918.

Litophyllus luteus (Barrows).

♀ Sugar Grove, Ohio, Oct. 26, 1918.

Pæcilochroa montana Emerton.

Put-in-Bay, Ohio, July 12, 1920.

Running in grass on lawn near State Fish Hatchery.

Sergiolus variegata (Hentz).

♂ Cedar Point, Ohio.

CLUBIONIDÆ.

Agræca pratensis Emerton.

♀ Columbus, Ohio, Nov. 7, 1917.

Anyphæna saltabunda Hentz.

♂ ♀ Rockbridge, Ohio, June 3, 1922.

Taken while sweeping above cliffs in Andropogon prairie.

Cæloles hybridus Emerton.

♂ Rockbridge, Ohio, Sept. 30, 1917.

AGELENIDÆ.

Cybæus silicis Barrows.

♂ ♀ Bainbridge, Ohio, Aug. 17, 1917.

DICTYNIDÆ.

Amaurobius ferox Emerton.

♂ Columbus, Ohio, April 28, 1919.

Dictyna bicornis Emerton.

♂ ♀ Columbus, Ohio, May 14, 1918.

All live on ground, under edges of stones, in dry, hot situations.

Dictyna volucripes Emerton.

♂ Delaware, Ohio, May 17, 1918.

Taken while sweeping in tall grass near a stream.

Lathys foxi (Marx).

♂ Flint, Ohio.

Taken in a bed of leaves in a deep ravine near a stream.

THERIDIIDÆ.

Ceratinella atriceps Cambridge.

♂ Rockbridge, Ohio, May 4, 1918.

Ceratinella carinata Cambridge.

♂ ♀ Flint, Ohio, April 14, 1918.

Taken under leaves in ravine.

Ceratinella formosa Banks—*Idionella formosa* Banks.

♀ Columbus, Ohio, Oct. 16, 1917.

Ceratinella pygmæa Emerton.

♂ South Columbus, Ohio, Oct. 16, 1917.

Ceratinopsis laticeps Emerton—*xantippe* Keyserling.

♂ ♀ Columbus, Ohio, Oct. 1, 1918.

Taken in wet pasture under boards and grass.

Grammonota inornata Emerton.

♂ ♀ Columbus, Ohio, May 2, 1918.

Grammonota ornata Cambridge.

♀ Rockbridge, Ohio, May 4, 1918.

Taken among grasses and sedges in swampy place in a valley.

Grammonota vittata Barrows.

♂ ♀ Hebron, Ohio, Oct. 3, 1918.

Taken near the edge of the canal sweeping in grass and weeds.

Lophocarenum crenatum Emerton.

♂ Columbus, Ohio, July 12, 1918.

Taken while sweeping on aviation field (river flat).

Theridium cinerium Emerton.

♀ Buckeye Lake, Ohio, June 24, 1917.

Taken under rotten log near the lake.

Tmeticus astivalis Emerton. = *Oedothorax oxypæderotipus* Crosby.

♂ Rockbridge, Ohio, May 4, 1918.

♂ Flint, Ohio, April 28, 1918.

Taken under leaves and stones near stream in deep, wooded, shale ravine.

Tmeticus maximus Emerton.

♂ ♀ Rockbridge, Ohio, Sept. 14, 1918.

Taken under wet stones under waterfall in ravine.

Tmeticus plumosus Emerton.

♂ Columbus, Ohio, May 2, 1918.

Taken under straw in field on side of hill.

LINYPHIIDÆ.

Bathypantes formica Emerton.

♂ Columbus, Ohio, June.

Bathypantes unimaculata Banks.

♂ ♀ Columbus, Ohio, Oct. 20, 1917.

Under logs in moist pastures, and under vegetation near sluggish streams in pastures or low ground.

Bathypantes zebra Emerton—*decorata* Banks.

♀ Flint, Ohio, April 14, 1918.

♂ ♀ Rockbridge, Ohio, May 4, 1918.

In the fall these spiders are found on the under side of webs spread in the curled up leaves in low, moist ravines in the woods.

Microneta latidens Emerton.

♂ ♀ Sugar Grove, Ohio, Oct. 26, 1918.

Microneta quinquedentata Emerton.

♂ Hebron, Ohio, Oct. 3, 1918.

Taken under overhanging bank, a few inches from the water of the canal.

Microneta viaria Blackwall.

♂ ♀ Rockbridge, Ohio, May 4, 1918.

♂ Columbus, Ohio, Oct. 8, 1919.

Taken under leaves and stones in a deep, wet ravine.

TETRAGNATHIDÆ.

Mysmena bulbifera Banks. = *Glenognatha bulbifera* (Banks).

♂ Columbus, Ohio.

♂ Orland, Ohio, June 3, 1918.

Lives in horizontal orb webs two inches above the ground in grass-land and weedy places.

Pathygnatha brevis Keyserling.

♂ ♀ Columbus, Ohio, Oct. 16, 1918.

Pathygnatha xanthostoma McCook (not Koch).

♂ ♀ Columbus, Ohio, Jan. 25, 1919.

EPEIRIDÆ.

Epeira foliata Hentz.

♂ Rockbridge, Ohio, July 27, 1917.

THOMISIDÆ.

Oxyptila americana Banks.

♀ Columbus, Ohio, July 3, 1917.

Xysticus discoursans Keyserling.

♂ ♀ Columbus, Ohio, May 8, 1918.

Xysticus elegans Keyserling.

♂ Flint, Ohio, May 27, 1918.

Xysticus graminis Emerton.

♂ Columbus, Ohio, May 8, 1918.

Xysticus ontariensis Emerton.

♂ ♀ Rockbridge, Ohio, Sept. 13, 1918.

Taken while sweeping in dry, upland prairie.

LYCOSIDÆ.

Pirata febriculosa? Beck.

♂ ♀ Rockbridge, Ohio, June 16, 1917.

♀ Sandusky, Ohio, July 31, 1917.

Schizocosa saltatrix (Hentz).

♂ ♀ Rockbridge, Ohio, March 27, 1921.

Running in leaves in open oak woods above cliffs.

Trochosa rubicunda Keyserling = *Lycosa polita* Emerton.

♀ Ashtabula County, Ohio.

ATTIDÆ.

Dendryphantes æstivalis Peckham.

♂ Rockbridge, Ohio, June 18, 1916.

Dendryphantes flavipedes Peckham.

♂ ♀ Rockbridge, Ohio, May 4, 1918.

Icius minutus Banks.

♂ ♀ Columbus, Ohio, May 8, 1918.

Pellenes jucundus Peckham.

♀ Rockbridge, Ohio, May 4, 1918.

Phidippus ardens Peckham.

♂ Columbus, Ohio, Sept. 7, 1919.

Probably the same as the males which Peckham describes from Oklahoma.

Zygoballus nervosus Peckham.

♂ Hebron, Ohio, Oct. 3, 1918.

The number of species previously recorded for Ohio, together with those of this list, brings the total up to 306 species.

They are distributed by families as indicated in the following table:

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Dysderidæ.....	2
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Agelenidæ.....	11
Dictynidæ.....	14
Theridiidæ.....	57
Linyphiidæ.....	22
Mimetidæ.....	1
Tetragnathidæ.....	10
Epeiridæ.....	34
Uloboridæ.....	2
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